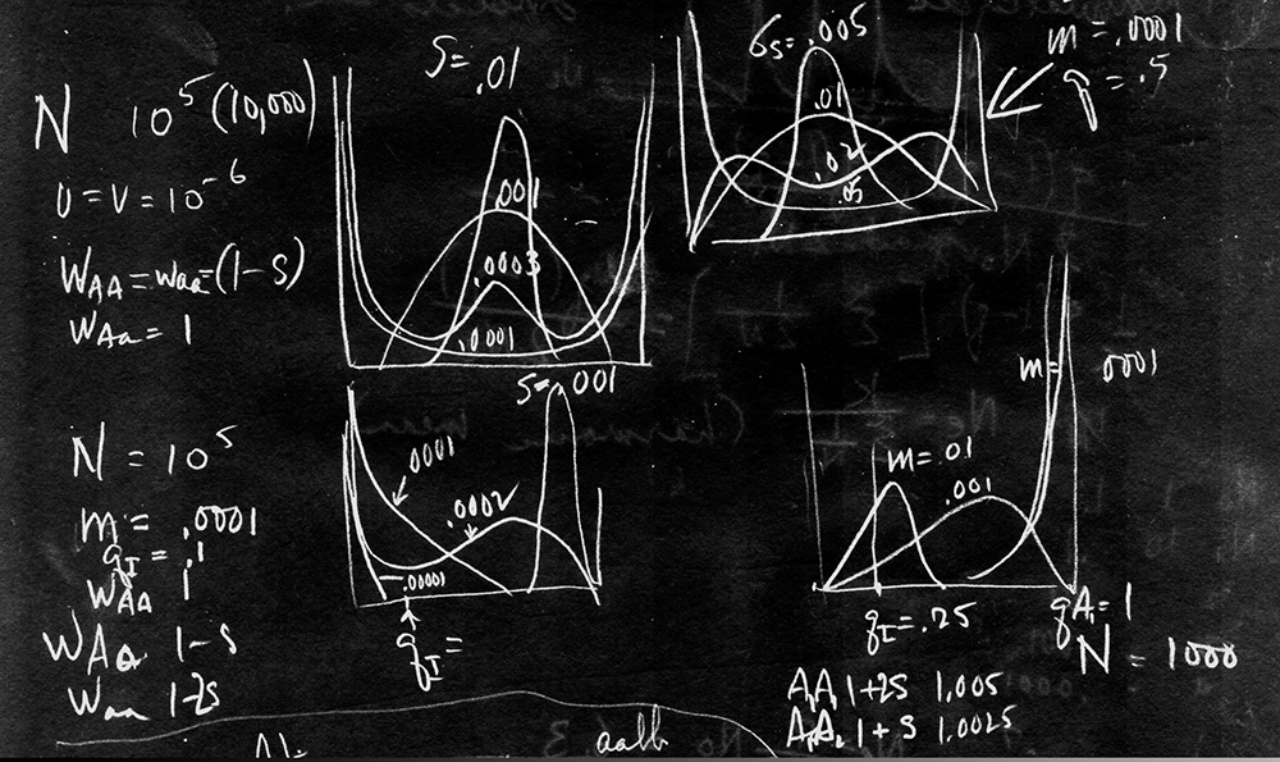

SEWALL WRIGHT TAUGHT ME

1. EVOLUTION

JOE CAIN
EDITOR

EUSTON GROVE PRESS

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PREFACE

Bob Sloan was a mentor during my doctoral studies at the University of Minnesota in the years around 1990. Knowing my interest in the synthesis period in evolutionary biology, Bob made a habit of presenting me with books, reprints, stories, and items related to that period and its personalities.

While helping organize his home study in the early 1990s, Bob presented me with a set of lecture notes he made during student days at the University of Chicago. "They might have some value," Bob suggested.

Throughout my career, I've seen good research on what was taught in classrooms frustrated by a lack of direct evidence. For instance, how did the teaching of evolution change in classrooms over the 1920s, before and after the 1925 Scopes Trial? Or, how was nature study assimilated into zoology and botany courses in the late 19th century? Did Robert Edmond Grant include transmutation in his lectures at the University of London? What did Dobzhansky, Anderson, and Mayr say in their Jesup lectures at Columbia University? People far more clever than I am have worked hard on these questions, extracting an extraordinary amount of information from indirect sources. But always they come back to the need for direct evidence documenting day-to-day activities in the classroom. What did lecturers *actually say* in their courses? What information *in fact* was presented? To answer these questions, student notes are essential primary sources. Frustratingly, they seem to the among the first things consigned to the dust bin of history.

The "they taught me" series aims to counter the lacuna of direct evidence about the classroom. It will publish historically valuable materials, especially student notes, to assist further scholarly study.

Joe Cain
London 2007

INTRODUCTION

Sewall Wright taught throughout his long career. Between 1926-1955, he worked at the University of Chicago. During this time, he developed and taught both undergraduate and graduate courses. By the early 1930s, Wright's teaching load settled into a core set of four courses: *Fundamental Genetics* (Zoology 310), *Biometry* (311), *Physiological Genetics* (312), and *Evolution* (313). He first taught *Evolution* in 1931. The term in which it was scheduled varied depending on Wright's other activities (Provine 1986: 170-175).

The lecture notes reproduced here relate to Wright's *Evolution* course, as presented in June-August 1951. These notes were made by Robert E. Sloan. At the time, Sloan was a master's student with an interest in paleontology and evolution.[1] His research paper for the course, reproduced in the Appendix, reflects this emphasis.

Famously, Wright was not a charismatic lecturer. Mayr (1992) commented on this regarding professional meetings. Provine (1986) noted the same with reference to classroom teaching. Sloan's own account confirms these reports:

> *Sloan*: …Sewall Wright was a very mild mannered gentleman who would stand there looking hurt and blinking when his students would not come to the obvious conclusions – obvious to him from the analysis that he put on the blackboard. He would cover the entire blackboard of a 30 foot wide classroom, 3 times a lecture.
>
> *Cain*: With simple math? Or complicated math?
>
> *Sloan*: With oh, nothing very complicated. It was nothing beyond algebra. He never got into either differential or integral calculus. A little bit of statistics. It is just that it was perpetual equations. And I was able to follow them really quite well. [Joe Cain] has my notes on the course, and

Table 1. Dates of Wright's *Evolution* Lectures

lecture date	*Sloan's page*	*lecture date*	*Sloan's page*
[25 June 1951]	1	[01 August 1951	[56]
[29 June 1951]	[3]	03 August 1951	59
02 July 1951	9	07 [sic: 06] August 1951	64
06 July 1951	13	08 August 1951	66
09 July 1951	18	10 August 1951	70
13 July 1951	19	13 August 1951	74
16 July 1951	23	15 August 1951	75
[20 July 1951]	[26]	17 August 1951	77
23 July 1951	35	20 August 1951	80
25 July 1951	39	27 August 1951	85
27 July 1951	45	29 August 1951	87
[30 July 1951]	[54]	loose notes	88

> basically, they consist of transcriptions of the equations that he wrote on the blackboard, together with some cryptic notes as to what these equations actually meant.[2]

Lecture notes are convoluted historical artifacts. Sloan's notes seem to cover Wright's lectures without omission, though this is difficult to verify independently. Separating (a) information coming directly from Wright and (b) Sloan's transformations can be difficult. The first half of these notes seems most like direct transcription, matching Sloan's recollections of rather mindless copying in an effort to keep up. Towards the end of the course more filtering seems imposed. As topics approached Sloan's own interests, doodling occurs and the notes appear to be more aids-to-memory than faithful transcriptions.

The numerical sequence written in the upper right corner of most pages is Sloan's own. His dating of individual lectures has gaps (Table 1). Some dates and breaks have been estimated by the editor; these are noted in [ ] brackets. The two pages of loose notes at the end of the set provide case studies focusing on "isolation by distance". These relate to material covered either on page 62 or page 87. The list of books opposite page 50 is dated to the week of 30 July by internal evidence: the references at the bottom of the page to upcoming activities.

Sloan's course assignments survive, too. Three exercises in mathematical population genetics were required. Sloan's worked solutions are given in the Appendix. Assignment 1 appears on pages 13-14. The solutions to Assignment 2 appear on pages 31-33, but note Sloan completed only

three of the four items. Assignment 3 appears following page 50. This includes not only the assignment itself, but also some preliminary work by Sloan, and an answer key (pages 51-54). The final examination paper is provided in the Appendix. Sloan's completed examination does not survive.

Historians of the synthesis period will find much of interest in these notes. For instance, during his first lecture, Wright gave a broad context in which the course was set (page 1). Predictably, *Genetics and the Origin of Species* was set as a supplemental text to the course, and approximately half the course consisted of mathematical population genetics. Midway through the course, Wright gave a list of readings relevant to the research paper he required (follows page 50). This is an exemplary illustration of the synthesis canon put to use in post-WW2 American evolutionary biology. The emphasis on Simpson in Wright's coverage of the evolution of higher categories (pp. 77-84) is fascinating, contradicting claims that Simpson's approach to mega-evolution was wholly abandoned. Wright's discussion of research on brain evolution (p. 87) also merits further study. Tilly Edinger's (1897-1967) research program is examined in Buchholtz and Seyfarth (1999).

These notes were made in pencil on paper. Some pages have deteriorated badly. Images have been adjusted to enhance legibility. The originals are held by the editor.

Notes

[1] Sloan received each of his four academic degrees from the University of Chicago: PhB in Liberal Arts (1948), BS in Geology (1950), MS in Geology (1952) and PhD in Geology (1953). He describes the atmosphere at the University of Chicago both in autobiographical material (Sloan 1996) and in oral history interviews (see note 2).

[2] Sloan, Robert E. 1996. "Interview with Robert E. Sloan by Joe Cain," Oral history interview. Tape 8, Side 1, March 14, 1996. Transcript on-line <www.ucl.ac.uk/sts/cain/projects/sloan>, revised: January 2001.

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Buchholtz, Emily A., and Ernst-August Seyfarth. 1999. The gospel of the fossil brain: Tilly Edinger and the science of paleoneurology. *Brain Research Bulletin* 48 (4):351-361.

Mayr, Ernst. 1992. Controversies in Retrospect. *Oxford Surveys in Evolutionary Biology* 8:1-34.

Provine, William. 1986. *Sewall Wright and Evolutionary Biology*. Chicago: University of Chicago Press.

Sloan, Robert E. 1996. *Autobiography of Robert Evan Sloan*. Manuscript published on-line <www.ucl.ac.uk/sts/cain/projects/sloan>.

LECTURE NOTES

Def gen + Origin Spp. ← Supplement to Course (1)

Fisher R.A. Genetical theory N. Sel.
Haldane J.B.S. Causes of Evol.
Goldschmidt. Material basis Evol.
Huxley Evol in Syn
Mayr Sys. & O. Spp.
Simpson T + M.
Stebbins G.L. '50 Variation + Evol in Plant
Gregory W.K. Evol. emerging
Wright S. 1931 Genetics 16: 97-159
39 Stat Gen. in relation to Evol.
Exposés de Biométrie et de la stat hist #802
48 Evol., Organ. E. Brit 8: 915-29
Gen of Pop " 10: 111 —
'49 Gs & Evol Ch 20
'49 Pop structure in evol Proc Am. Phil So,
93: 471-478
'51 Genetical Str. of Pop. Ann. Eugenics
15: 323-354

Term Paper
Evol at level of
1 gene

(1) Genetics of Populations
A Property of randomly breeding populations
1 Gene frequencies
1, 2, multiple loci
2 Systematic pressures
a mutational pressure Δq
b Selection pressure σ
c Immigration "
(b with basket)
3. Fluctuations $\delta_{\Delta q}$; $\sigma^2_{\delta q}$

2. dd Evol of Mitosis - Meiosis

3 Ind Org. Most of course here —
Genetics of Evolution.

4 Distribution of gene frequency (result of 2 & 3) ②

{Δq=0} = equilibrium

0 ——— 0% A ——— 100% A

5 Phenotypic meaning

B. Population structure (natural pop's do not conform to system in A)

1. Inbreeding Coefficient

2. Hierarchic ~~breeding~~ structure

3. Island Model w/ low immigration

4. Isolation by distance uniform density & rare dispersal

C. Interplay of systematic & random processes.

2. Application of Pop Gen to Natural Groups.

A Nature of Spec. at lower levels

Genetics of variability within & between spp & ssp.

B Nature of Higher Categories, homology & analogy

C. Evolutionary cycle emergence, adaptive rad.

selection between higher categories (intergroup competition)

D Genetics of Homology

E Theories of Evol

Philosophy of Evolution.

Possible term papers (5)

look for marine snail gen freq on shelf.

Homology of Gene Action
Polyploidy + origin Spp
gen. diff. in Spp cross (specific groups)
Natural Variability in Spp (" ")
Gene frequency in Spp (" ") ✓ blood grps
Experimental studies in Selection (coloration etc) in mat
Isolation mechanisms
Nature of Spp. ; SSpp in groups ; clines, rings
Natural selection of color in foxes
Polymorphism (a number of alleles = numerous)

Major Steps in Evolution

Presumably life began w/ gene self duplication but imperfectly occasionally (mut.)
seem to be ephemerally Nucleoproteins

I Origin of gene — autocatalytic molecule

1 Evolution along single lineage by mutation

$A \rightarrow A' \rightarrow A'' \rightarrow A'''$

$A''' \rightarrow A' \checkmark$
$A''' \rightarrow A''$

store of organic material in absence of life
exhaustion, Selection

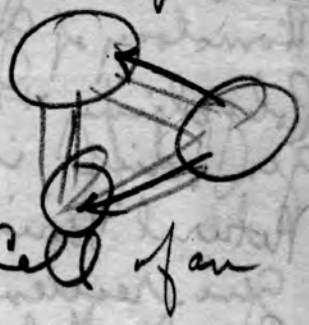
$\rightarrow^{1} \rightarrow^{2} \rightarrow^{3} \rightarrow^{4}$ ornithine $\rightarrow^{5}$ citrulline $\rightarrow^{6}$ arginine $\rightarrow^{7}$

mutation to convert unused org. molecule to one that has been used up catalytically favorable

2. Evol of population of genes through selection in addition to mutation probably not trend toward stable genes
& chemical stability

mutation pressure
selection pressure (synthetic capacity or predation
Impression from surrounding regions

3 Symbiotic systems of gene, Evolution of the array of local populations



I Origin of equationally dividing Cell of an assemblage of genes

Subcat. same as I but more scope for evol.

III Interbreeding Spp. - cells capable of conjugation
* reduction. possibility of recombination

previously 100 mutations means 10^{6} genotypes
now " means 2^{100} " "
10^{30}

300 mut

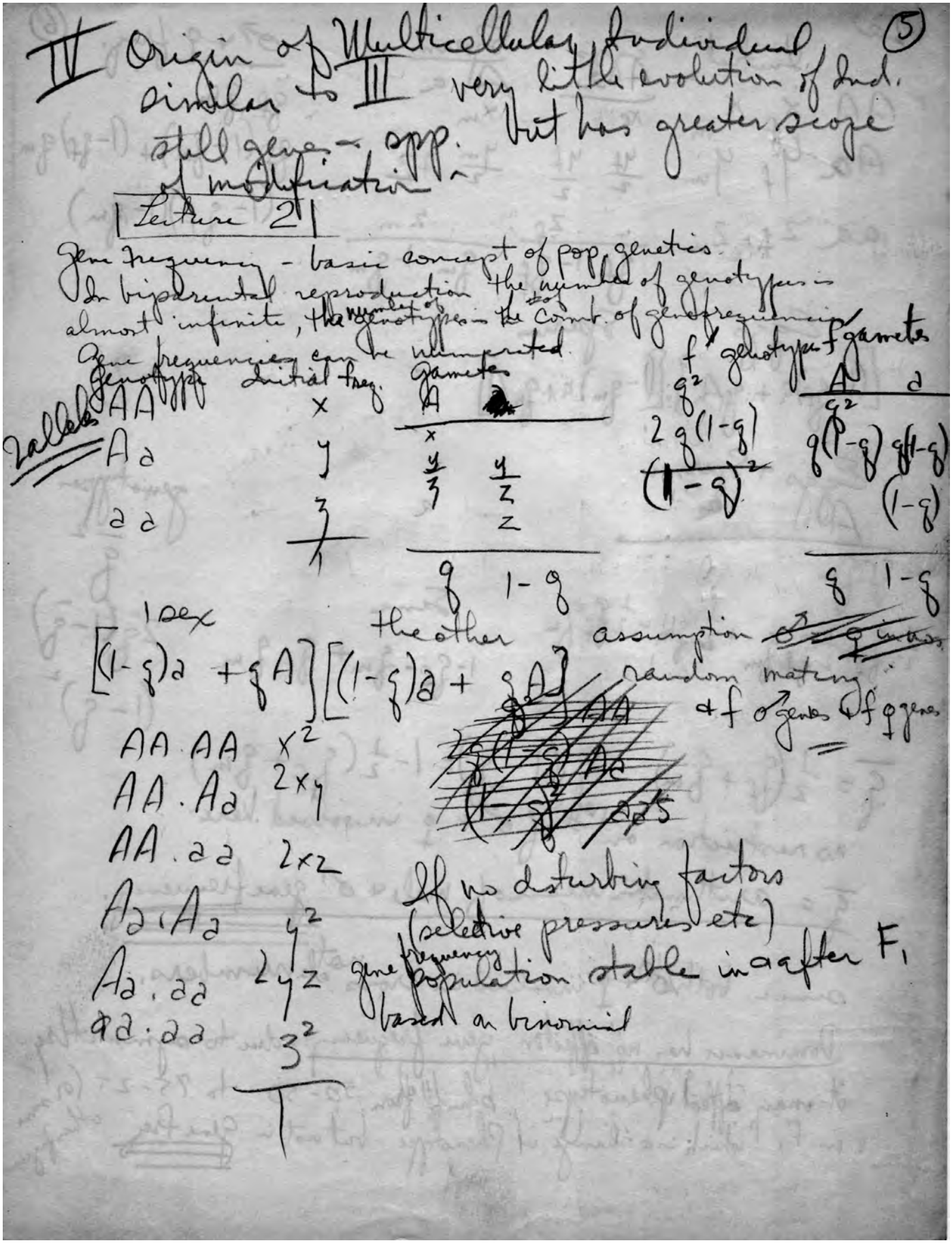
$2^{300} = 10^{90}$ more than ± of part in visible universe.

1 Evol along one lineage a succession of mut.
2. Evol of a Spp. according to Pop structure
A Uniparental reprod. (w/o conjugation
(Selection among clones, persistent genotypes)

B Exclusive Biparental reprod. → eff. panmixia
(Selection by average effect of allele

C. Array of partially isolated populations
continual process of diff + intergroup recombination.

Lethal constituents in Spermatium.



IV Origin of Multicellular Individual (5)
similar to III very little evolution of Ind.
still gene ~ opp. but has greater scope
of modification

Lecture 2

Gene frequency - basic concept of pop genetics.
In bisexual reproduction the number of genotypes is almost infinite, the number of gametes is not. The comb. of gene frequencies

Gene frequencies can be interpreted

Genotypes Initial freq. Gametes

		A	a
AA	x	x	
Aa	y	y/2	y/2
aa	z		z
	1	q	1-q

f genotype f gametes

		A	a
q^2		q^2	
$2q(1-q)$		$q(1-q)$	$q(1-q)$
$(1-q)^2$			$(1-q)$
		q	1-q

alleles

1 sex

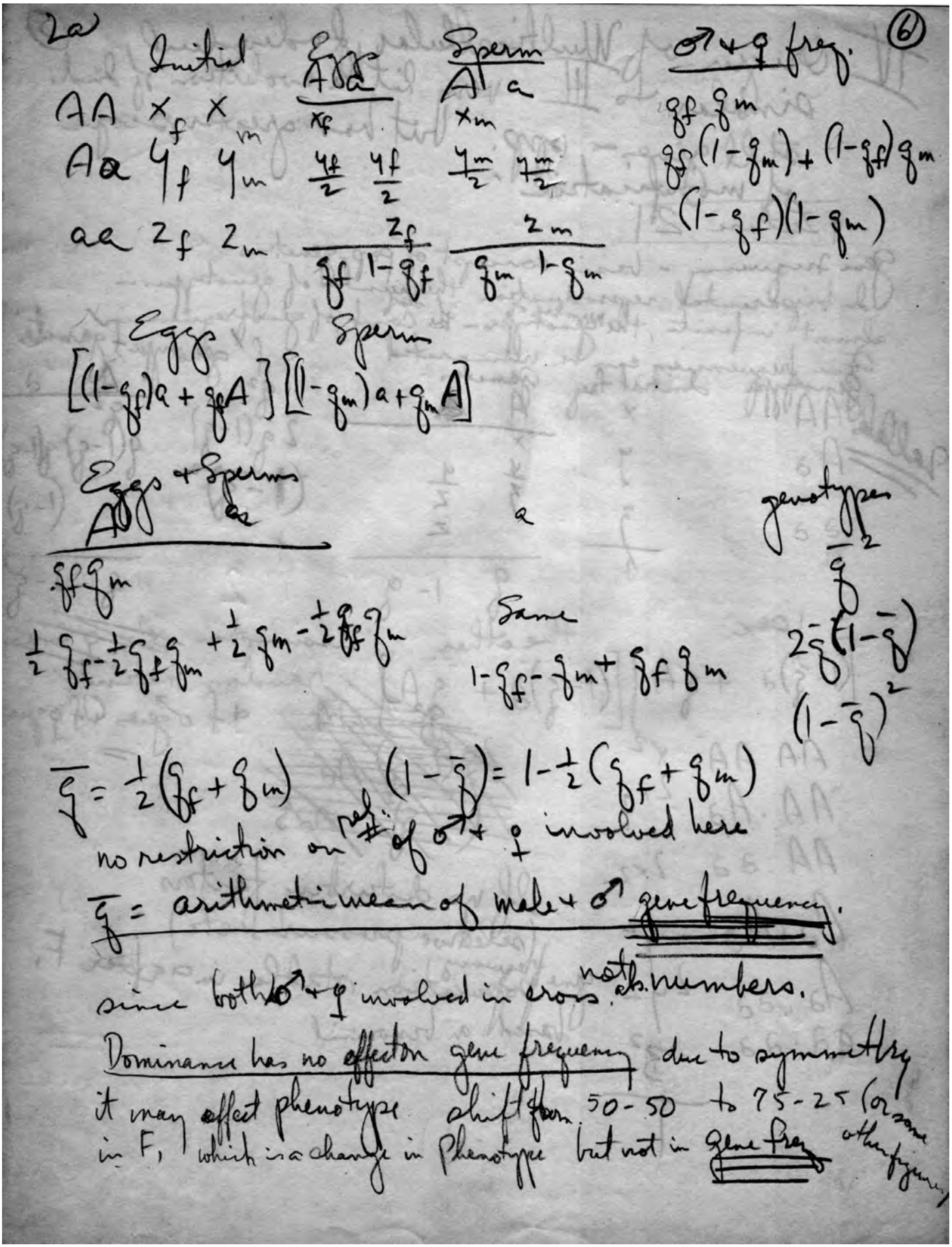
$[(1-q)a + qA][(1-q)a + qA]$

the other assumption random mating

f of gens of q gens

AA . AA x^2
AA . Aa $2xy$
AA . aa $2xz$
Aa . Aa y^2
Aa . aa $2yz$
aa . aa z^2

If no disturbing factors (selective pressures etc) gene frequency population stable in after F_1
based on binomial


2a
Initial
Eggs
Sperm
♂ + ♀ freq.
⑥
AA
Aa
aa
Eggs
Sperm
Eggs + Sperms
genotypes
Same
Same
no restriction on # of ♂ + ♀ involved here
= arithmetic mean of male + ♂ gene frequency.
since both ♂ + ♀ involved in cross.
not sh. numbers.
Dominance has no effect on gene frequency due to symmetry
it may affect phenotype
shift from 50-50 to 75-25 (or some other frequency)
in F1 which is a change in phenotype but not in gene freq

(7)

Hardy G.H. 1908 Science 28: 49-50
Weinberg W. 1908 Jahreshefte d. Verf. vaterländische Naturkunde in Württemburg 64: 368-382

Multiple alleles

quite common if not most common.

many different type alleles

isoallele

allele subscript instead of superscript to avoid conf. w/exp.

A_1 ← allele

Ind. pop.	Gametes
A_1A_1	f_{11}
A_1A_2	f_{12}
⋮	⋮
A_1A_n	f_{1n}
A_2A_2	f_{22}
A_2A_n	f_{2n}
A_nA_n	f_{nn}

$A_1\ A_2 \cdots A_n$

$q_1 = f_{11} + \frac{1}{2}(f_{12} + f_{13} \cdots f_{1n})$

$q_2 = f_{22} + \frac{1}{2}(f_{12} + f_{23} \cdots f_{2n})$

$q_n = f_{nn} + \frac{1}{2}(f_{1n} + f_{2n} \cdots f_{(n-1)n})$

$\overline{q} = \frac{1}{2}(q_{1f} + q_{1m})$

frequencies in Eggs + sperms

random mating

2

$[q_1A_1 + q_2A_2 \cdots q_nA_n]$

$[q_1A_1 + (1-q_1)A_0]$ treating all other isoalleles as one allright except when conducting tests that distinguish them

Equil. population

q_1

$2q_1q_2$

$2q_1q_n$

q_2

$2q_2q_n$

q_n^2

replacing back in order

$q_1 = q_1^2 + q_1q_2 + q_1q_3 \cdots q_1q_n$

$= q_1[q_1 + q_2 + q_3 \cdots q_n]$ (compound symbols)

$= q_1$

(6)

Gene frequency of sex-linked genes

Jennings HS 1916 genetics 1: 53-89

♀ XX

♂ X, or XO

$q_m = q_f$

gene frequency of ♂ = q of ♀ preceding generation (prime here)

$q_f = \frac{1}{2}(q'_f + q'_m)$

$q = x q_f + (1-x) q_m$

$q = \frac{x}{2}(q'_f + q'_m) + (1-x) q'_f$

$q \leftrightharpoons q'$

$q' = x q' + (1-x) q'_m = q$

$\left[\frac{x}{2} + 1 - x\right] q'_f = x$

$1 - \frac{x}{2} = x$

$x = 2/3$

$\bar{q}$ = stable freq.

$\bar{q} = \frac{2}{3} q_f + \frac{1}{3} q_m$

however equilibrium not be derived immediately

$q_m - \bar{q} = q'_f - \frac{2}{3} q'_f - \frac{1}{3} q'_m$

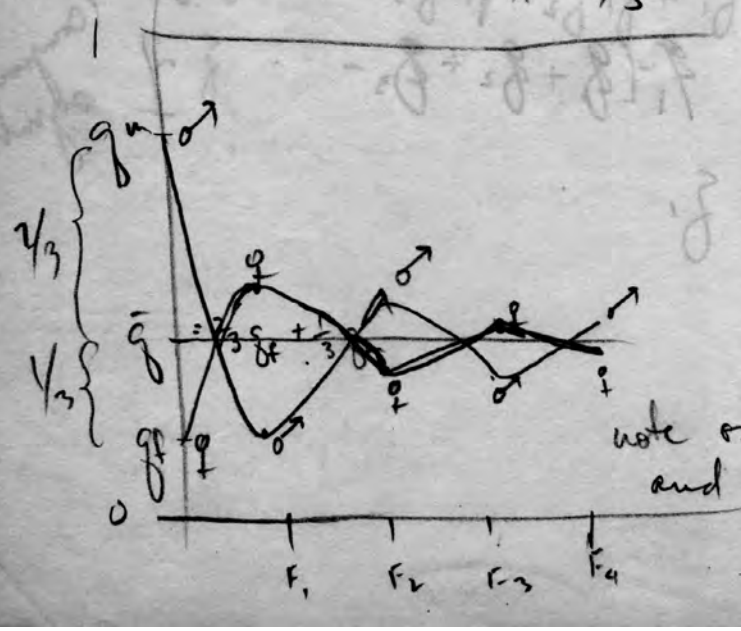
$= \frac{1}{3} q'_f - \frac{1}{3} q'_m$

$= \left(\frac{1}{3} q'_f + \frac{1}{6} q'_m\right) - \frac{1}{2} q'_m$

$= \frac{1}{2} \bar{q} - \frac{1}{2} q'_m$

$q_m - \bar{q} = -\frac{1}{2}(q'_m - \bar{q})$

$q_f - \bar{q} = -\frac{1}{2}(q_f - \bar{q})$



note oscillatory approach to $\bar{q}$ and $q_m = q_f$

in 10 generations .001 away from $\bar{q}$

(9)

Description of population genotypic a

$(g_{A_1}A_1 + g_{A_2}A_2 \cdots g_{A_n}A_n)^2 (g_{B_1}B_1 \cdots g_{B_n}B_n)^2 (\quad)$

$(g_{B_1}B_1 \cdots g_{B_n}B_n)^2$

$\left[\sum_{i=1}^{n_A} g_{A_i} A_i\right]^2 \left[\sum_{i=1}^{n_B} g_{B_i} B_i\right]^2$

first terms

---

certain cases reach equilibrium immediately (July 2 '51 from Turntull)

No linkage ♂ AABB & ♀ aabb

F_1 Aa Bb

$[\frac{1}{2}a + \frac{1}{2}A]^2 [\frac{1}{2}b + \frac{1}{2}B]^2$ (product principle of probabilities)

the equilibrium freq would be reach imm. & maintain

But this is not always the case

F_1

AABB ♂ > ¼ AABB
AABB ♀

½ AaBb

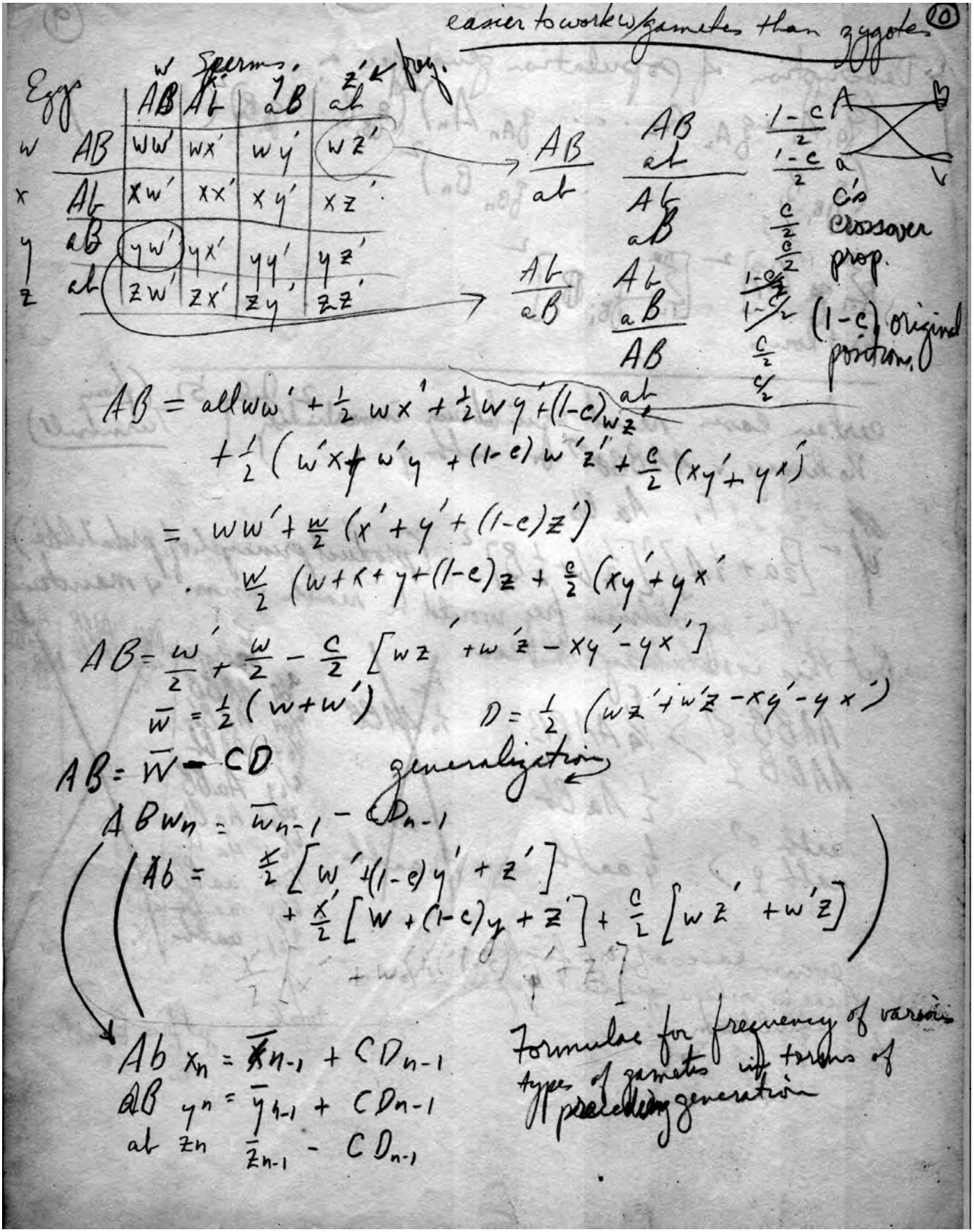
aabb ♂ > ¼ aabb
aabb ♀

F_2	type
9/64	AABB
6/64	AABb
1/64	AAbb
6/64	AaBB
20/64	AaBb
6/64	Aabb
1/64	aaBB
6/64	aaBb
9/64	aabb

totals

even in cases of no linkage there is only a gradual approach to equilibrium

get from Bader↑



easier to work w/ gametes than zygotes (10)

Eggs / Sperms

		AB	Ab	aB	ab
w	AB	ww′	wx′	wy′	wz′
x	Ab	xw′	xx′	xy′	xz′
y	aB	yw′	yx′	yy′	yz′
z	ab	zw′	zx′	zy′	zz′

AB / ab
Ab / aB

AB		
ab		
Ab	$\frac{1-c}{2}$	C's
aB	$\frac{1-c}{2}$	C's
Ab	$\frac{c}{2}$	crossover
aB	$\frac{c}{2}$	prop.
Ab	$\frac{1-c}{2}$	(1-c) original
aB	$\frac{1-c}{2}$	positions.
AB	$\frac{c}{2}$	
ab	$\frac{c}{2}$	

$$AB = \text{all } ww' + \tfrac{1}{2} wx' + \tfrac{1}{2} wy' + (1-c) wz'$$
$$+ \tfrac{1}{2}\left(w'x + w'y + (1-c) w'z' + \tfrac{c}{2}(xy' + yx')\right.$$
$$= ww' + \tfrac{w}{2}(x' + y' + (1-c)z')$$
$$\tfrac{w}{2}(w + x + y + (1-c)z + \tfrac{c}{2}(xy' + yx'$$

$$AB = \frac{w'}{2} + \frac{w}{2} - \frac{c}{2}\left[wz' + w'z - xy' - yx'\right]$$

$$\bar{w} = \tfrac{1}{2}(w + w') \qquad D = \tfrac{1}{2}(wz' + w'z - xy' - yx')$$

$$AB = \bar{w} - cD$$

generalization

$$AB\,w_n = \bar{w}_{n-1} - cD_{n-1}$$

$$Ab = \tfrac{x}{2}\left[w' + (1-c)y' + z'\right] + \tfrac{x'}{2}\left[w + (1-c)y + z\right] + \tfrac{c}{2}\left[wz' + w'z\right]$$

$$Ab\ x_n = \bar{x}_{n-1} + cD_{n-1}$$
$$aB\ y_n = \bar{y}_{n-1} + cD_{n-1}$$
$$ab\ z_n = \bar{z}_{n-1} - cD_{n-1}$$

Formulae for frequency of various types of gametes in terms of preceding generation

(51) (11)

Sperm

$W_n = \bar{w}_{n-1} - c' D_{n-1}$
$x_n = \bar{x}_{n-1} + c D_{n-1}$
$y_n = \bar{y}_{n-1} + c D_{n-1}$
$z_n = \bar{z}_{n-1} - c D_{n-1}$

$\bar{w}_n = \bar{w}_{n-1} - \bar{c} D_{n-1}$
$\bar{x}_n = \bar{x}_{n-1} + \bar{c} D_{n-1}$
$\bar{y}_n = \bar{y}_{n-1} + \bar{c} D_{n-1}$
$\bar{z}_n = \bar{z}_{n-1} - \bar{c} D_{n-1}$

$\bar{c} = \frac{1}{2}(c + c')$

c' crossovers in prev. gen.

$$D_n = \frac{1}{2}\Big[\bar{w}_{n-1}\bar{z}_{n-1} - \bar{w}_{n-1} c' D_{n-1} - \bar{z}_{n-1} c D_{n-1} + c c' D^2_{n-1}$$
$$\bar{w}_{n-1}\bar{z}_{n-1} - \bar{z}_{n-1} c' D_{n-1} - \bar{w}_{n-1} c D_{n-1} + c c' D^2_{n-1}$$
$$- \bar{x}_{n-1}\bar{y}_{n-1} - \bar{x}_{n-1} c' D_{n-1} - \bar{y}_{n-1} c D_{n-1} - c c' D^2_{n-1}$$
$$- \bar{x}_{n-1}\bar{y}_{n-1} - \bar{y}_{n-1} c' D_{n-1} - \bar{x}_{n-1} c D_{n-1} - c c' D^2_{n-1}\Big]$$

$$\bar{w}_{n-1}\bar{z}_{n-1} - \bar{x}_{n-1}\bar{y}_{n-1} - \bar{c} D_{n-1} = D_n$$

$$\bar{w}_n \bar{z}_n - \bar{x}_n \bar{y}_n = \bar{w}_{n-1}\bar{z}_{n-1} - \bar{w}_{n-1}\bar{c} D_{n-1} - \bar{z}_{n-1}\bar{c} D_{n-1} + \bar{c}^2 D^2_{n-1}$$
$$- \bar{x}_{n-1}\bar{y}_{n-1} - \bar{x}_{n-1}\bar{c} D_{n-1} + \bar{y}_{n-1}\bar{c} D_{n-1} - \bar{c}^2 D^2_{n-1}$$

$$\bar{w}_{n-1}\bar{z}_{n-1} - \bar{x}_{n-1}\bar{y}_{n-1} - \bar{c} D_{n-1} = D_n = \bar{w}_n \bar{z}_n - \bar{x}_n \bar{y}_n$$

$$D_n = D_{n-1} - \bar{c} D_{n-1} = (1-\bar{c})^{n-1} D_1$$

or $(1-\bar{c}) D_{n-1}$
$(1-\bar{c})^2 D_{n-2}$
$(1-\bar{c})^3 D_{n-3}$ etc.

(12)

$$\bar{W}_2 = \bar{w}_1 - \bar{c}D_1 = \bar{w}_1 - D_1 + (1-\bar{c})D_1 = (\bar{w}_1 - D_1) + \bar{D}_2$$

$$\bar{W}_3 - \bar{D}_3 = \bar{W}_2 - \bar{D}_2 = \bar{W}_1 - \bar{D}_1$$

$$\bar{W}_\infty - \bar{D}_\infty = \bar{w}_1 - \bar{D}_1 \quad \therefore \bar{W}_\infty = \bar{w}_1 - \bar{D}_1 = \bar{w}_1 - (\bar{w}_1\bar{z}_1 - \bar{x}_1\bar{y}_1)$$

This = to. zero if any crossover exists at all

$$= \bar{w}_1^2 + \bar{w}_1\bar{x}_1 + \bar{w}_1\bar{y} + \bar{w}_1\bar{z}_1 - (\bar{w}_1\bar{z}_1 - \bar{x}\bar{y}_1)$$

$$= \bar{w}_1 + \bar{w}_1\bar{x}_1 + \bar{w}_1\bar{y}_1 + \bar{x}_1\bar{y}_1$$

$$= (\bar{w}_1 + \bar{x}_1)(\bar{w}_1 + \bar{y}_1) = q_A\, q_B$$

	B	b	
A	w	x	q_A
a	y	z	$1-q_A$
	q_B	$1-q_B$	

$\therefore$ equilibrium is approached assymptotically

$$w_n = \bar{w}_1 - D_1[1-(1-c)(1-\bar{c})^{n-2}]$$
$$w'_n = \bar{w}_1 - D_1[1-(1-c)(1-\bar{c})^{n-2}]$$
$$\bar{w}_n = \bar{w}_1 - D[1-(1-c)^{n-1}]$$

Ds express departures from random combination

$$D_n = (1-\bar{c})D_{n-1}$$
$$D_n = (1-\bar{c})^{n-1} D_1$$

If no linkage at all $\bar{c} = \frac{1}{2}$; $D_n = \frac{1}{2} D_{n-1}$

$$D_n = (1-\bar{c})^{n-1} D_1$$

$$(1-\bar{c})^x = \frac{1}{2} \longrightarrow x \log(1-\bar{c}) = \log \frac{1}{2}$$

$$x = \frac{\log_e \frac{1}{2}}{\log_e (1-\bar{c})} = \frac{-.693}{-(\bar{c} + \frac{\bar{c}^2}{2} + \frac{\bar{c}^3}{3} + \frac{\bar{c}^4}{4} \ldots)}$$

$= \frac{.693}{\bar{c}}$ for small values of $\bar{c}$ 10 or less

at $\bar{c} = .10$ 6.6
$\bar{c} = .01$ 69.
$\bar{c} = .001$ 693.

Thus in population which have been breeding populations for any length of time geologically there is equilibrium w/respect to genes A+a + B+b

2 factor case Wentworth W. 1909 ZIAV 1:277-330
Robbins RB 1918 Genetics 3:375-389
3 factor Jennings H 1944 Amer. Math Stat 15:25-57
(+ extension to any # of genes + alleles) 1948 Genetics 33:548-564

.01 .01 .10 .10
A B C ABC ♀
a b c a b c ♂

nonrovers ABC abc
single ABc aBC AbC abc
double rovers AbC aBc

$c_1 = .10$
$c_2 = .10$
$c_{12} = 0$

generation

0	.4000	.0500	.000
1	.3650	.0650	.0050
2	.3350	.0770	.0110
5	.2627	.1004	.0315
10	.2028	.1165	.0633
20	.1502	.1241	.1015
50	.1260	.1250	.1240
100	.1250	.1250	.1250

$c_1 = .01$
$c_2 = .01$
$c_{12} = 0$

0	.49	.005	000
1	.4852	.0074	.00005
2	.4804	.0098	.0001
5	.4664	.0165	.0005
10	.4446	.0270	.0015
20	.4055	.0449	.0047
30	.3169	.0813	.0205
50	.2306	.1091	.0512
100	.1599	.1229	.0943
500	.1266	.1250	.1234
1000	.1250	.1250	.1250

Friday 6 July 51
Assignment # 1

(1) Find gene frequencys at equilibrium

	♀	♂	♀	♂	♀	♂
AA	70	70	80	10	20	40
Aa	0	0	0	0	40	40
aa	30	30	20	10	140	20
	100	100	100	20	200	100

(14)

(2) What is the proportion of heterozygotes in the following? assuming equilibrium. A_ both homo & heterozygote

A_	9900	9999	256
aa	100	1	144
	10000	10000	400

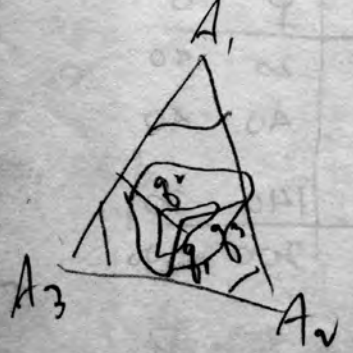
(3)

also	♀	♂	♀	♂
+/+	300	+/y 0	+/+ 600	+/y 200
+/w	0	0	+/w 200	0
w/w	0	w/y 100	w/w 200	w/y 300
	300	100	1000	500

800 CCAa ♀♀ 200 CcAA ♂♂ Equilibrium freq?
200 CCaa ♀♀ 300 ccAA ♂♂

Deduce freq of 9 genotypes from following equilibrium

900 C_A_	agouti	.9
60 C_aa	black	.06
40 cc__	white	.04
1000		



102
122
18
194
140
44.5
23.5

(15)

Cattle
Red = RR
Roan Rr
white rr

	Red	Roan	White	obs	calc
Red x Red	1710	(102)	(39)	1851	1998
Red x Roan	1763	1336	(15)	3114	3620
Red x White	20	891	(8)	729	724
Roan x Roan	664	1275	471	2410	1642
Roan x White	(8)	168	72	248	657
White x White	(4)	(8)	141	153	64
	4169	3980	756	8705	

$\frac{214}{8705}$ = 2.5% ∴ assume a 2 factor hypothesis

this still gives some exceptions $\frac{114}{8705}$ = 1.3%
still another possible

	PP	Pp	pp
RR		Roan	Red
Rr			
rr	White		

	R_2R_2	R_2r_2	r_2r_2
R_1R_1		Red	
R_1r_1		Roan	
r_1r_1			White

Parents

This gives $\frac{43}{8705}$ = 0.5%

obs.		Calc
44.5	red	46.2
47.1	roan	43.5
8.5	white	10.2

offspring obs	Calc
47.9	48.4
43.4	42.3
8.7	9.2

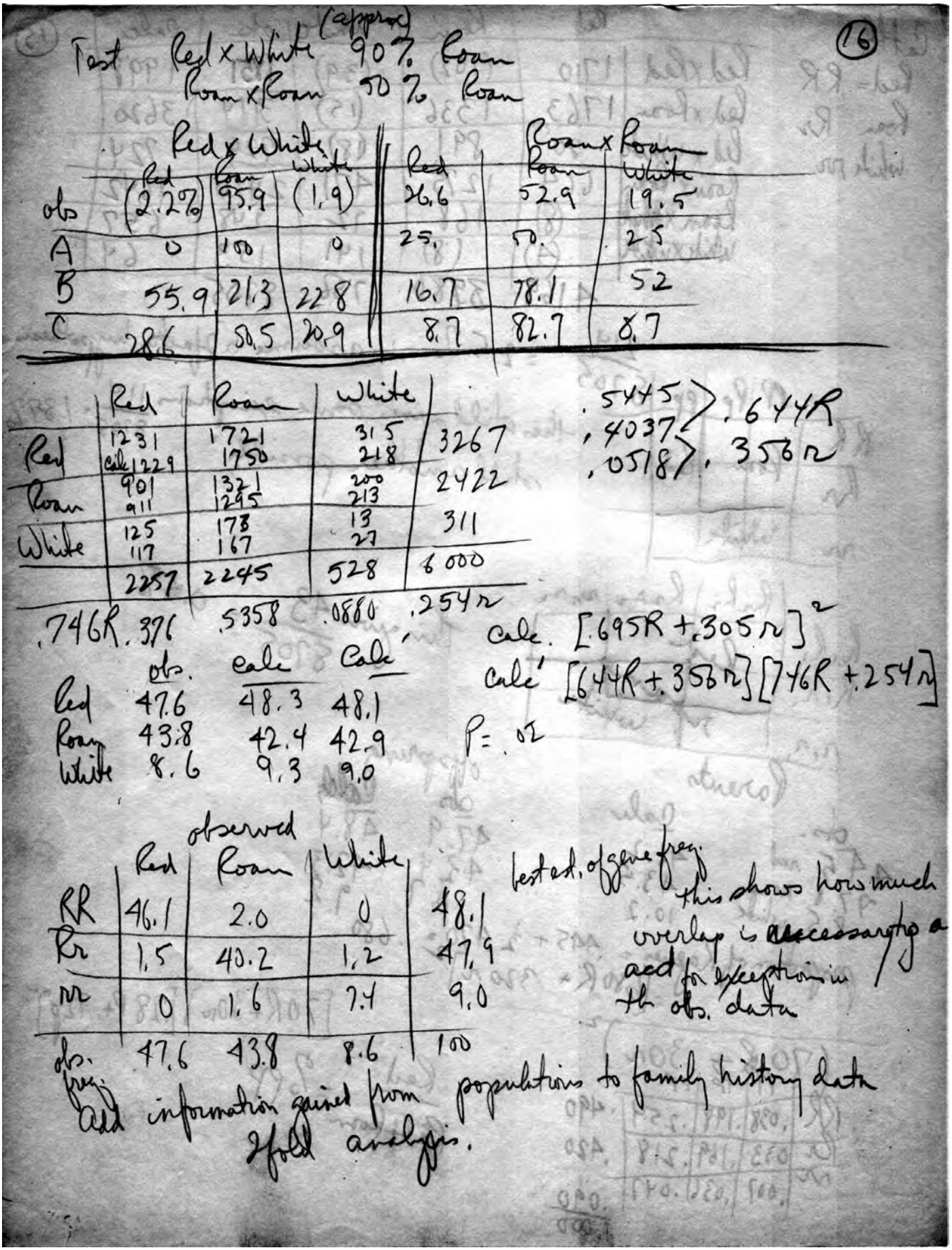
proportion of R genes = .445 + ½ .470 = .680

$= [.680R + .320r]^2$

$[.70R + .30r]^2 [.28P + .72p]^2$

$(.70P + .30r)^2$	PP	Pp	pp	
RR	.038	.198	.254	.490
Rr	.033	.169	.218	.420
rr	.007	.036	.047	.090
				1.000

$\frac{\text{Red}}{\text{Red + Roan}}$ = % PP



(16)

Test Red x White (approx) 90% Roan
Roan x Roan 50% Roan

	Red x White: Red (2.2%)	Roan	White (1.9)	Roan x Roan: Red	Roan	White
obs		95.9		26.6	52.9	19.5
A	0	100	0	25.	50.	25
B	55.9	21.3	22.8	16.7	78.1	5.2
C	28.6	50.5	20.9	8.7	82.7	8.7

	Red	Roan	White	
Red	1231 calc 1229	1721 1750	315 218	3267
Roan	901 911	1321 1295	200 213	2422
White	125 117	178 167	13 27	311
	2257	2245	528	6000

.5445 > .644R
.4037 > .356r
.0518

.746R .376 .5358 .0880 .254r

	obs.	calc	Calc'
Red	47.6	48.3	48.1
Roan	43.8	42.4	42.9
White	8.6	9.3	9.0

calc. $[.695R + .305r]^2$
calc' $[.644R + .356r][.746R + .254r]$

P = .02

observed

	Red	Roan	White	
RR	46.1	2.0	0	48.1
Rr	1.5	40.2	1.2	47.9
rr	0	1.6	7.4	9.0
obs.	47.6	43.8	8.6	100
exp.				

tested. of gene freq.
this shows how much overlap is necessary to account for exceptions in the obs. data

Add information gained from populations to family history data
2 fold analysis.

(17)

Population principles Man O, A, B, AB blood groups

cells	agglut. serum A	agglut. serum B
O	aB	0 0
A	-B	0
B	a-	0
AB	--	

Bernstein ΣIAV 37:237

suggested 3 allele hyp.

Von Dungern & Hirschfeld suggest 2

O	aabb	OXO → O
A	A-bb	AXA → AO
B	aaB-	BXB → BO
AB	A-B-	ABXAB → anything

Bernstein also brought in pop. data

OO	ii		
AA AO	$I^A I^A$, $I^A i$		
BB BO	$I^B I^B$, $I^B i$	$I^A I^B$	
AB	$I^A I^B$	A B O	

i Has since been discovered that A can be split but lumped here.

$[(1-s)A + sa]^2 [(1-t)B + tb]^2$; $[r(i) + p(I^A) + q(I^B)]^2$

Von P. + Hers. hyp. Bernstein hyp.

OO	$s^2 t^2$	r^2
AA; AO	$(1-s^2)t^2$	$p^2 + 2pr$
BB; BO	$s^2(1-t^2)$	$q^2 + 2qr$
AB	$(1-s^2)(1-t^2)$	$2pq$

$s = \sqrt{O + B}$, $t = \sqrt{O + A}$ } good estimates for these freq.

$r = \sqrt{O}$
$r + p = \sqrt{O + A}$
$r + q = \sqrt{O + B}$
$p + q + r = 1$

11,588

	obs.	Calc V.D.+H	Calc Bernstein
O	32.5	$s^2 t^2$ = 37.4	r^2 = 32.3
A	37.6	$(1-s^2)t^2$ 32.7	$p^2 + 2pr$ 37.8
B	20.9	$s^2(1-t^2)$ 16.0	$q^2 + 2qr$ 21.1
AB	9.0	$(1-s^2)(1-t^2)$ 13.9	$2pq$ 8.8
	100	χ^2 = 50.8	100

P not given in table very bad

$\chi^2 = 1$

$p = .31$

(18)

1346 Javanese VD+H Bernstein

O	39.9	45.2	41.0
A	25.7	20.4	24.6
B	29.0	23.7	27.9
AB	5.4	10.7	6.5

$\chi^2 = 4.15$

	Prob 7.05	Prob .005 – .05	Prob <.005	
			63	67
VD+H	2	2		
			11	17
Bernstein	48	8		

total evidence tend to support assumption of multiphalleles.

Monday 9 July 51 | further illust. of genetics humans.

Race RR. 1950 Cold Spring Hbr. S. Quant Biol 15: 207

9 loci available for study in man

Blood group genes

1. ABO 1900
   $A_1 A_2$
2. MN 1927
   $M_S M_s N_S N_s$ 1947
3. Pp 1927
4. Taste Phenol thio carbamide
5. Secretes ABO$_a$ antigen in saliva 1932
   Lewis Le^a Le^b 1946
6. Rh, rh at least 10 alleles 1940
7. Lutheran Lu 1945
8. Kell K 1946
9. Duffy Fy 1950

MN series Landsteiner & Levenson 1927+28 J Exp. Med (19) 48:731
no agglutinins found in this series (Inject to rabbit y antibodies found
Sera separated.)

a days lecture on gene frequency in humans
w/ examples.

factors which chang gene frequency: —

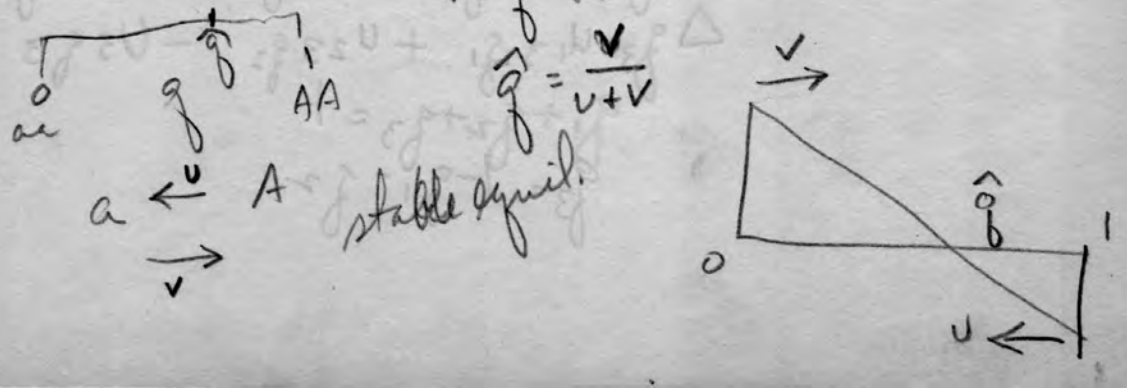
I Immediate
1. systematic Δq (determinate in Principle
a recurrent mutation
b immigration + crossbreeding
c. ~~selection~~ (systematic intrusion work)
2 Fluctuation in gene freq. δq indet σ_q^2 determinate
abc as in 1 above
d. accidents of sampling
3. Unique events
alte

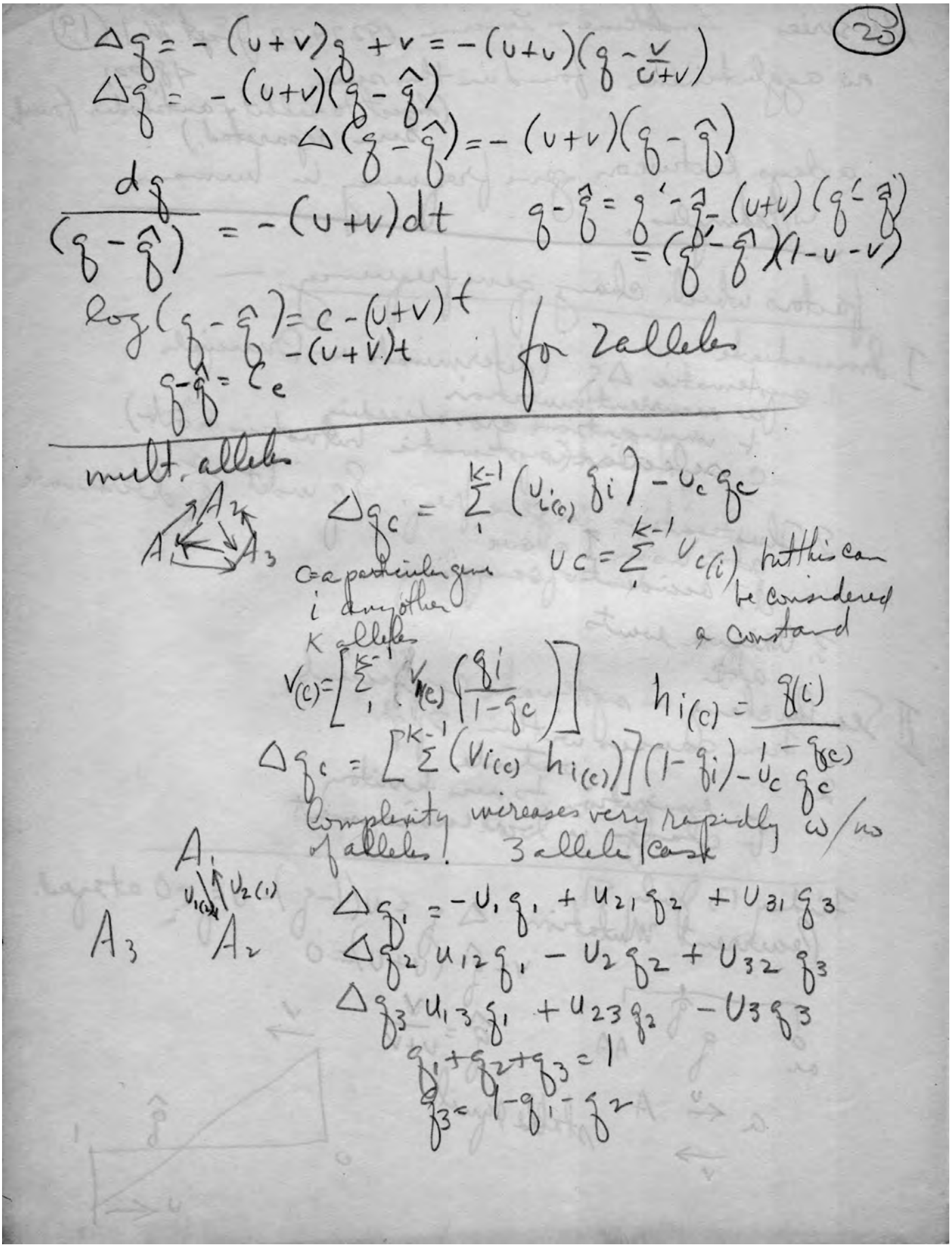
II Secular chang in systematic coefficients
1 from causes within spp.
2. outside
a. emigration to new territory
b change in local environment

Friday 13 July 51
Recurrent Mutation $\Delta q = v(1-q) - uq = 0$ at equil.

$v = \hat{q}(u+v) = 0$

$\hat{q} = \frac{v}{u+v}$




23
$\Delta q = -(u+v)q + v = -(u+v)(q - \frac{v}{u+v})$
$\Delta q = -(u+v)(q - \hat{q})$
$\Delta(q - \hat{q}) = -(u+v)(q - \hat{q})$
$\frac{dq}{(q - \hat{q})} = -(u+v)dt$
$q - \hat{q} = q' - \hat{q}' = (u+v)(q' - \hat{q}')$
$= (q - \hat{q})(1 - u - v)$
$\log(q - \hat{q}) = c - (u+v)t$
$q - \hat{q} = \varepsilon_e^{-(u+v)t}$
for 2 alleles
mult. alleles
A_1 A_2 A_3
$\Delta q_c = \sum_1^{k-1} (u_{i(c)} q_i) - u_c q_c$
c = a particular gene
i any other
K alleles
$u_c = \sum_1^{k-1} u_{c(i)}$ but this can be considered a constant
$v_{(c)} = \left[\sum_1^{k-1} v_{i(c)} \left(\frac{q_i}{1 - q_c}\right)\right]$
$h_{i(c)} = \frac{q_{(i)}}{1 - q_{(c)}}$
$\Delta q_c = \left[\sum^{k-1} (v_{i(c)} h_{i(c)})\right](1 - q_i) - u_c q_c$
Complexity increases very rapidly w/ no of alleles! 3 alleles/case
A_1
$u_{1(2)}$ $u_{2(1)}$
A_3 A_2
$\Delta q_1 = -u_1 q_1 + u_{21} q_2 + u_{31} q_3$
$\Delta q_2 \; u_{12} q_1 - u_2 q_2 + u_{32} q_3$
$\Delta q_3 \; u_{13} q_1 + u_{23} q_2 - u_3 q_3$
$q_1 + q_2 + q_3 = 1$
$q_3 = 1 - q_1 - q_2$
$\hat{q}$
1
u

(2-1)

$$\Delta q_1 = -(v_1 + u_{31})q_1 + (u_{21} - u_{31})q_2 + u_{31} = 0$$

$$\Delta q_2 = (u_{12} - u_{32})q_1 - (u_2 + u_{32})q_2 + u_{32} = 0$$

$$\hat{q}_1 = \frac{u_{31}u_2 + u_{31}u_{32} + u_{32}u_{21} - u_{32}u_{31}}{D}$$

$$= \frac{u_2 u_{31} + u_2 u_{32} - u_{21}u_{32} - u_{23}u_{32} - u_2 u_{32} + u_{32}u_{21}}{D}$$

$$\hat{q}_1 = \frac{u_2 u_3 - u_{23}\ u_{32}}{\sum^{3} [u_j\, u_A - u_{j<k}\, u_{i<j}}$$

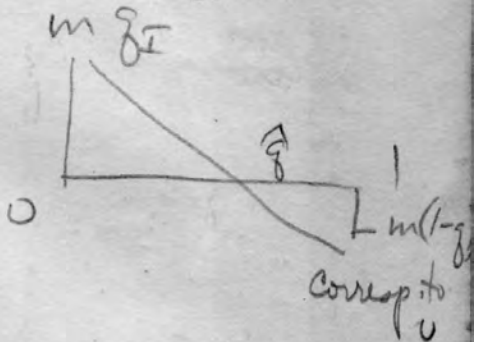
given only as illust.

Immigration pressure

corr. to v

$$q_I \xrightarrow{m} q$$

$$\Delta q = -m(q - q_I)$$



$$\Delta q = m q_I (1-q) - m(1-q_I)q$$

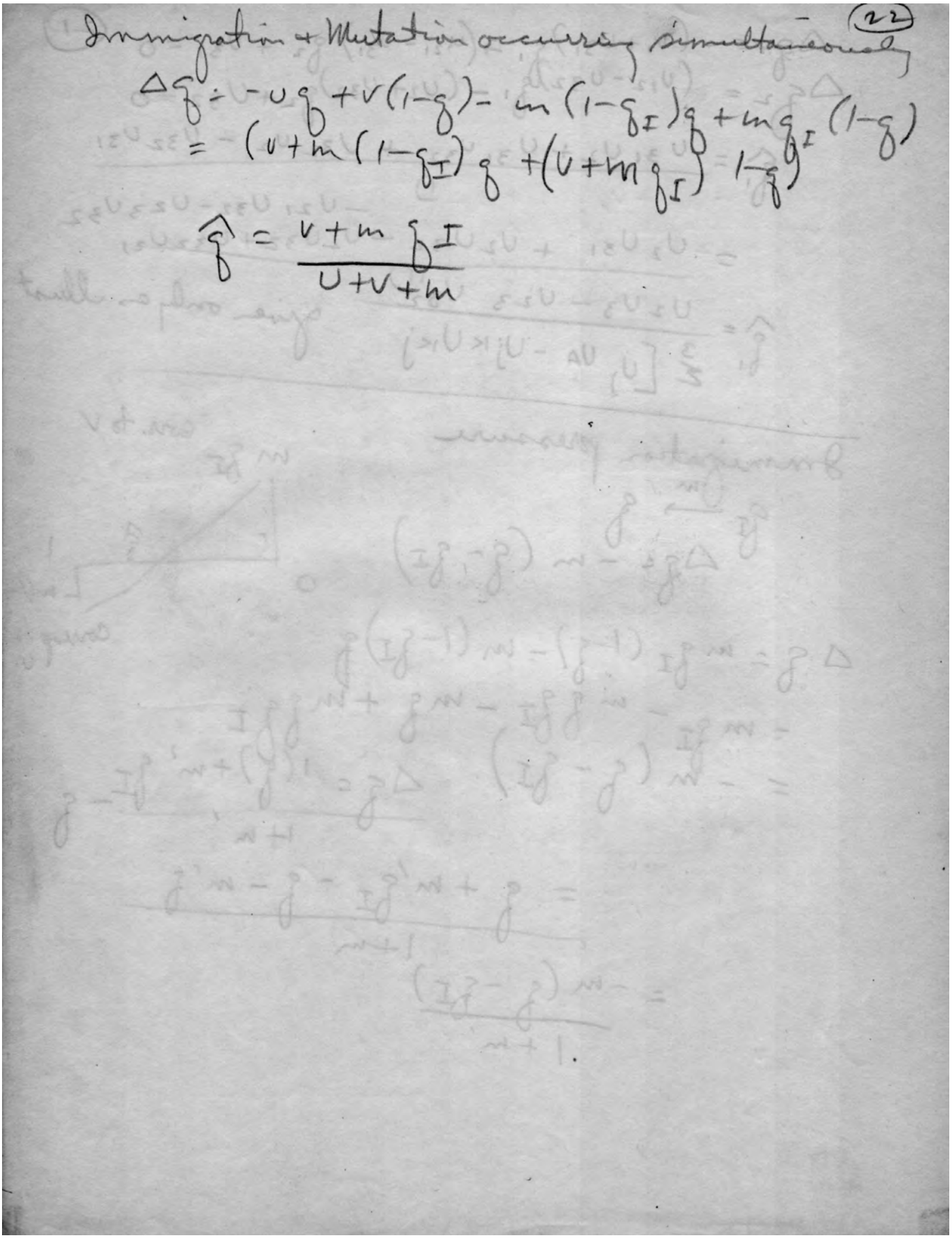
$$= m q_I - m q q_I - m q + m q q_I$$

$$= -m(q - q_I)$$

$$\Delta q = \frac{1(q) + m' q_I}{1+m'} - q$$

$$= \frac{q + m' q_I - q - m' q}{1+m}$$

$$= \frac{-m(q - q_I)}{1+m'}$$


Immigration + Mutation occurring simultaneously (22)
$\Delta q = -uq + v(1-q) - m(1-q_I)q + mq_I(1-q)$
$= (v + m(1-q_I))q + (v + mq_I)(1-q)$
$\hat{q} = \frac{v + m q_I}{u+v+m}$

(23)

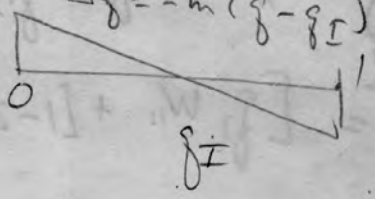
16 July '51

Box 523
Powell Wyo.

(2) A_1A_1 1.002 A_1 mutates to A_2 at
A_1A_2 1.001 rate 10^{-5}/generation
A_2A_2 1.000

$$\Delta q = -uq + v(1-q)$$

recurrent mutation



$$\Delta q = -uq + v(1-q) - m(1-q_I)q + mq_I(1-q)$$

$$\hat{q} = \frac{v + mq_I}{u + v + m}$$

Selection

Population of haploids

Key genotype	q	w adaptive value
A_1	q_1	w_1
A_2	q_2	w_2
A_3	q_3	w_3

$$\bar{w} = \Sigma qw$$

$$\Delta q_1 = \frac{q_1 w}{\Sigma qw} - q_1 = \frac{q_1 w}{\bar{w}} - q_1 = q_1\left[\frac{w - \bar{w}}{\bar{w}}\right]$$

new value q_1

Population of diploids

genotype	q	w
A_1A_1	q_1^2	w_{11}
A_1A_2	$2q_1q_2$	w_{12}
A_2A_2	q_2^2	w_{22}

Gene A_1 q_1 $\left[q_1^2 w_{11} + q_1 q_2 w_{12}\right]/q_1$

Gene A_2 q_2 $\left[q_2^2 w_{22} + q_1 q_2 w_{12}\right]/q_2$

$$q_1^2 + q_1 q_2 = q_1(q_1 + q_2) = q_1$$

$$\bar{w} = q_1^2 w_{11} + 2q_1 q_2 w_{12} + q_2^2 w_{22}$$

$$\Delta q_1 = q_1[w_1 - \bar{w}]/\bar{w}$$

(2-1)

$$\Delta q_1 = q_1\left[\frac{w_1-\bar{w}}{\bar{w}}\right] = \frac{\left[q_1^2 w_{11} + q_1 q_2 w_{12} - q_1 \bar{w}_{11} - 2q_1^2 q_2 w_{12} - q_1 q_2^2 w_{22}\right]}{\bar{w}}$$

$$= q_1\left[q_1(1-q_1)w_{11} + (1-2q_1)q_2 w_{12} - q_2^2 w_{22}\right]/\bar{w}$$

$$= q_1(1-q_1)\left[q_1 w_{11} + (1-2q_1)w_{12} - (1-q_1)w_{22}\right]/\bar{w}$$

$$\bar{w} = q_1^2 w_{11} + 2q_1(1-q_1)w_{12} + (1-q_1)^2 w_{22}$$

$$\frac{d\bar{w}}{2dq_1} = \left[q_1 w_{11} + (1-2q_1)w_{12} + (1-q_1)w_{22}\right]$$

(both q and $(1-q)$ are necessary in Δq formula)

$$\Delta q_1 = \frac{q_1(1-q_1)}{2\bar{w}}\,\frac{d\bar{w}}{dq_1} \quad \text{if } w\text{'s are constant}$$

$$\Delta q_1 = \frac{q_1(1-q_1)}{2\bar{w}}\,\Sigma\left[w\frac{df}{dq_1}\right] \quad \text{but } w \text{ maybe } f(q) \text{ then}$$

Genotype	f	w
A_1A_1	q_1^2	$c(1+S_{11})$
A_1A_2	$2q_1q_2$	c
A_2A_2	q_2^2	$c(1+S_{22})$

choosing w_{12} as standard
$S_{11}+S_{22}$ are selective advantages of $w_{11}+w_{22}$ over w_{12} (or under)

$$\bar{w} = c\left[1 + S_{11}q_1^2 + S_{22}(1-q_1)^2\right]$$

$$2\frac{d\bar{w}}{dq_1} = c\left[2S_{11} - 2S_{22}(1-q_1)\right]$$

$$\Delta q_1 = \frac{c\,q_1(1-q_1)\left[S_{11}q_1 - S_{22}(1-q_1)\right]}{\bar{w}}$$

since $S_{11}+S_{22}$ are usually small (1 or 2%)

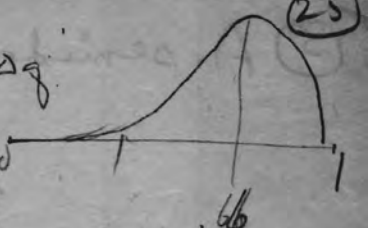
then this can be reduced to $\bar{w} = c$ +

$$\Delta q_1 = q_1(1-q_1)\left[S_{11}q_1 - S_{22}(1-q_1)\right]$$ to an approximation

(25)

① favorable
A_1 recessive ($S_{11} > 0$, $S_{22} = 0$)

$\Delta q_1 = S_{11} q_1^2 (1 - q_1)$



$\frac{d\Delta q}{dq_1} = 2q_1 - 3q_1^2 = 0$

$q_1 = 2/3$

② A_1 unfavorable dom. $S_{11} = 0$, $S_{22} > 0$

$\Delta q_1 = -S_{22} q_1 (1 - q_1)^2$

③ A_1 semidominant fav. $S_{22} = -S_{11}$ $\Delta q_1 = S_{11} q_1 (1 - q_1)$

④ $S_{11} + S_{22}$ same sign (heterosis)

$\hat{q} = \frac{S_{22}}{S_{11} + S_{22}}$

$\Delta q_1 = (-S_{11} + S_{22}) q_1 (1 - q_1)(\hat{q}_1 - q_1)$

3 stable configurations

$A_2 \xrightarrow{v} A_1$ w/selection against A_1

$\Delta q_1 = v(1 - q_1) - q_1(1 - q_1)(S_{11} q_1 + S_{22}(1 - q_1))$

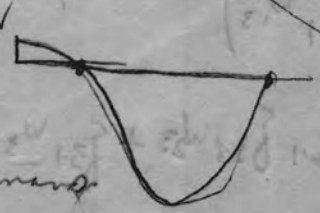
A_2 ← this one just too unstable, location of ~~midpoint~~ $\hat{q}$ depends on S_{12}

S_{11} neg.

① A_1 recess., ($S_{22} = 0$)

$\Delta q = v(1 - q) - S_{11} q_1^2 (1 - q)$

$\hat{q}^2 = \frac{v}{S_{11}}$



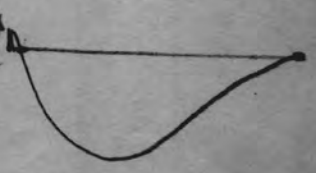
example - albinism in humans

② A_1 unfav. dom. ($S_{11} = 0$)

$\Delta q_1 = v(1 - q) - S_{22} q_1 (1 - q_1)^2$

$q_1(1 - \hat{q}_1) = \frac{v}{S_{22}}$

$\hat{q} = \frac{v}{S_{22}}$ approx.



(3) A. semidominant $S_{22} = -S_{11}$

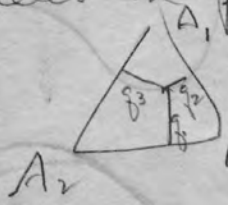
$$\Delta q_1 = v(1-q_1) - S_{22} q_1 (1-q_1)$$

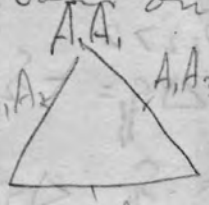
$$\hat{q} = \frac{v}{S_{22}} \text{ exactly}$$

(26)

Multiple alleles & selection.

3 alleles on percentage basis on $\triangle$ as in Petr.





3 alleles genotype	f	Rel. value	
A_1A_1	q_1^2	w_{11}	q_1^2
A_1A_2	$2q_1q_2$	w_{12}	$2q_1(1-q_1)q_{2\cdot1}$
A_1A_3	$2q_1q_3$	w_{13}	$2q_1(1-q_1)q_{3\cdot1}$
A_2A_2	q_2^2	w_{22}	$(1-q_1)^2 q_{2\cdot1}^2$
A_2A_3	$2q_2q_3$	w_{23}	$2(1-q_1)\,2(1-q_1)^2 q_{2\cdot1}$
A_3A_3	q_3^2	w_{33}	$(1-q_1)^2 q_{3\cdot1}$
	1		

$\left.\begin{matrix} 2q_1(1-q_1) \\ (1-q_1)^2 \end{matrix}\right\}$

$q_1^2 \quad \Delta q_1 = q_1(w_1 - \bar{w})/\bar{w}$

$q_{2\cdot1}$ (q_2 mid of q_1) $= \frac{q_2}{1-q_1}$

$q_{3\cdot1} = \frac{q_3}{1-q_1}$

fog of collective allele $A_2 + A_3$

$q_2 + q_3 = 1 - q_1$ / 1

W of collective alleles. treating as two allele case w/ A & all others the 2 alleles.

w_{11}

$(q_{2\cdot1} w_{12} + q_{3\cdot1} w_{13})$

$(q_{2\cdot1}^2 w_{22} + 2q_{2\cdot1} q_{3\cdot1} w_{23} + q_{3\cdot1} w_{33})$

(27)

$\Delta q_1 = q_1(1-q_1)\frac{\partial \bar{w}}{\partial q_1}\Big/ 2\bar{w}$ restricted to $w \neq f(q_1, 1-q_1)$

general ←

$\Delta q_1 = \frac{q(1-q_1)\Sigma w \frac{\partial f}{\partial q_1}}{2\bar{w}}$

$q_2 = q_{2\cdot 1}(1-q_1)$

$q_3 = q_{3\cdot 1}(1-q_1)$

$\frac{\partial q_3}{\partial q_1} = -q_{3\cdot 1}$ $\quad \frac{\partial q_2}{\partial q_1} = -q_{2\cdot 1}$

no of alleles

$\sum_{n=1} \Delta q_n = 0$

at equilibrium all $\Delta q = 0$ $\quad + \Delta q_1 = \frac{q_1(w_1 - \bar{w})}{\bar{w}} = 0$

$w_1 = \bar{w} = w_2 = w_3$ at equil.

f w $\bar{w} = 1 - S_1 q_1^2 - S_2 q_2^2 - S_3 q_3^2 \quad (= \Sigma f w)$

A_1A_1	q_1^2	$1-S_1$
A_1A_2	$2q_1q_2$	1
A_1A_3	$2q_1q_3$	1
A_2A_2	q_2^2	$1-S_2$
A_2A_3	$2q_2q_3$	1
A_3A_3	q_3^2	$1-S_3$
	1	

$\frac{\partial \bar{w}}{\partial q_1} = -2S_1 q_1 - 2S_2 q_2 \frac{\partial q_2}{\partial q_1} - 2S_3 q_3 \frac{\partial q_3}{\partial q_1}$

$= -2S_1 q_1 + 2S_2 q_2 q_{2\cdot 1} + 2S_3 q_3 q_{3\cdot 1}$

$= -2S_1 q_1 + \frac{2S_2 q_2^2}{1-q_1} + \frac{2S_3 q_3^2}{1-q_1}$

$\Delta q_1 = \frac{-q_1(S_1 q_1 - S_1 q_1^2 - S_2 q_2^2 - S_3 q_3^2)}{\bar{w}} = 0$

(2) $\Delta q_2 = \frac{-q_2}{\bar{w}}(S_2 q_2 - \Sigma S q^2) = 0$

$\Delta q_3 = \frac{-q_3}{\bar{w}}(S_3 q_2 - \Sigma S q^2) = 0$ } at equil.

(28)

(b) $S_1 \hat{q}_1 = S_2 \hat{q}_2 = S_3 \hat{q}_3 = \Sigma S \hat{q}^2$

(a) $\hat{q}_1 = \dfrac{\Sigma S \hat{q}^2}{S_1}$ & symmetrically.

$= \dfrac{1/S_1}{\Sigma 1/S}$

If S's are all positive there is a stable equil.

$$\Delta q_1 = \frac{-S_1 q_1}{\bar{w}} (q_1 - \hat{q})$$

(derived from @ here & @ on prev. page.

If S's are all neg then there is an unstable equil. & the trend is toward one of the homozygotes heading toward the corners.

working w/ gene frequencies rather than zygotes as before, (just as valid.)

$$w_1 = \frac{(1-S_1)q_1^2 + q_1 q_2 + q_1 q_3}{q_1}$$

w_2

w_3

$\bar{w} = 1 - S_1 q_1^2$

$\bar{w} = 1 - \Sigma S q^2$

$$\Delta q_1 = \frac{q_1 (w_1 - \bar{w})}{\bar{w}}$$

$$= \frac{q_1 (1 - S_1 q_1 - 1 + \Sigma S q^2)}{\bar{w}}$$

$$= \frac{q (S_1 q_1 - \Sigma S q^2)}{\bar{w}}$$

$$w_1 = \frac{w_{11} q_1^2 + w_{12} q_1 q_2 + w_{13} q_1 q_3 + \cdots}{q_1 (q_1 + q_2 + q_3 + \cdots)} = w_{11} q_1 + w_{12} q_2 + w_{13} q_3 + \cdots$$

$= \xi(1)$

and w_1 is a weighted average of all the w's involving A_1

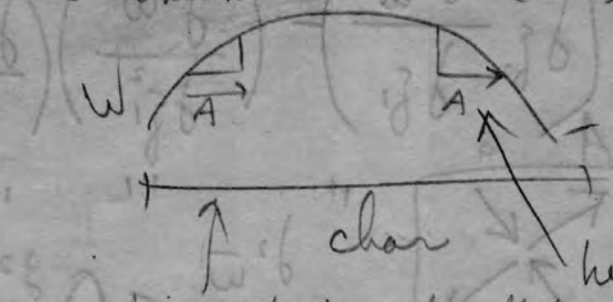
Multiple loci

Multiple factor analysis requires additive adaptive values which does not exist (??? desirability of using)

29

	w
A_1A_1	1.02
B_1B_2	1.05
C_2C_3	.92

$\bar{w} \neq 1.04$



Genotypes f Adaptive value f w

$A_1A_1B_1B_1$ $g_{A_1}^2 g_{B_1}^2$ $w_{A_1A_1B_1B_1}$

|| B_1B_2 $2 g_{A_1} g_{B_1} g_{B_2}$ $w_{A_1A_1B_1B_2}$

B_2B_2 $g_{A_1}^2 g_{B_2}^2$ $w_{A_1A_1B_2B_2}$

$\left(g_{A_1}^2\right)$

$g_{B_1}^2$ $w_{A_1A_1BB_1}$ B_1B_2 B_2B_2

$2 g_{B_1} g_{B_2}$

$g_{B_2}^2$

A_1A_2 B_1B_1 $2 g_{A_1} g_{A_2} g_{B_1}^2$

B_1B_2 " $2 g_{B_1} g_{B_2}$

|| B_1B_2 " $g_{B_2}^2$

etc

$2 g_{A_1} g_{A_2}$

A_2A_2 B_1B_1 $g_{A_2}^2$

B_1B_2

|| B_2B_2 " $2 g_{B_1} g_{B_2}$

" $g_{B_2}^2$

$\left(g_{A_2}^2\right)$

$\bar{w} = \Sigma f w$

Example to show magnitude of error introduced due to lack of randomness introduced by w's not being additive

	B_1B_1	B_1B_2	B_2B_2
A_1A_1	1	1−S	1−4S
A_1A_2	1−S	1	1−S
A_2A_2	1−4S	1−S	1

$g_{A_1} = 1/2$

$g_{B_1} = 1/2$

w AB
x Ab
y aB
z ab

$w = \frac{(S+c) - \sqrt{S^2+c^2}}{4S} = y$

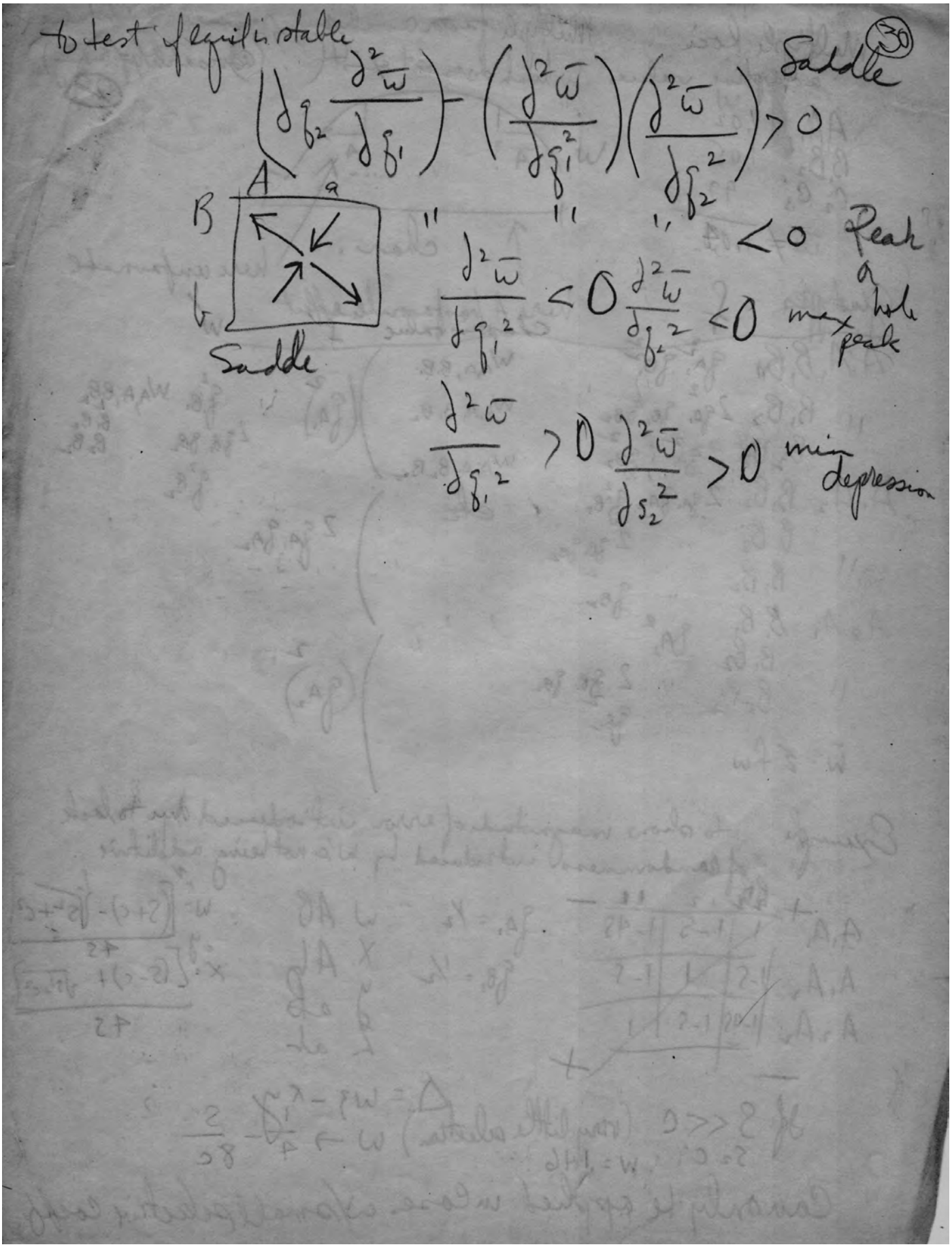
$x = \frac{(S-c) + \sqrt{S^2+c^2}}{4S}$

If $S \ll c$ (very little selection) $\Delta = wz - xy$

$S = c$ $w = .146$

$w \to \frac{1}{4} - \frac{S}{8c}$

Can only be applied in case w/small selective coeff.


to test if equil is stable
Saddle
A
B
a
b
Saddle
Peak
or
hole
max
peak
min
depression

(31)

Problems assignment 2

① $A_2 \rightarrow A_1$ 10^{-5} ; $A_2 \leftarrow A_1$ 10^{-6}

$\Delta q_1 = 10^{-5}(1-q_1) - 10^{-6} q_1$

$(\Delta q_1 = 0)\quad q_1 = \frac{10^{-5}}{10^{-5}+10^{-6}} = \frac{.00001 0}{.0000 11} = .909$

② $A_2 \leftarrow A_1$ 10^{-5}

A_1A_2 1.001 1+s ; A_2A_2 1 ; A_1A_1 1.002 (1+2s

$\Delta q_1 = -10^{-5} q_1 + \frac{(.001)}{s} q_1 (1-q_1)$

$q = q_1 = 0 \quad 1-q_1 = \frac{.00001}{.001} = .01 \quad q_1 = .99$

A_1A_1 q^2 1.002 ; A_1A_2 $2q(1-q)$ 1.001 ; A_2A_2 $(1-q)^2$ 1

$\bar{w} = 1 + .002 q_1^2 + .002 q_1 - .002 q_1^2$

$\bar{w} = \frac{1.002 q_1^2 + 1.001 q_1 (1-q_1)}{q_1}$

$= 1.002 q_1 + 1.001 (1-q_1)$

$\Delta q_1 = q_1 \left(\frac{w_1 - \bar{w}}{\bar{w}} \right)$

$= q_1 (1.001 -$

③ $a \xleftarrow{10^{-5}} A$

AA 1 ; Aa 1 ; aa 1-s 1-.01 q_a

$\Delta q_a = 10^{-5} q_a - (1-q_a) q_a$

$\bar{w} = 1 - .01 q_a^2$

$w_a = .99 q_a + (1-q_a)$

$= 1 - .01 q_a$

$\Delta q_a = \frac{q_a (1-s)}{2\bar{w}} \frac{d\bar{w}}{d q_a}$

$-.01 q_a^2 (1-q_a) = .9$

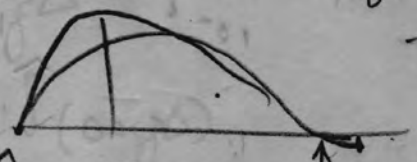
(32)

$\Delta q_a = .00001(1-q_a) + .01 q_a^2(1-q_a)$ $= u(q_A) - sq_a^2 q_A$

$- sq_a \cdot q_a q_A$

$\hat{q}_a = 1$

$\hat{q}_a = \frac{.00001}{.01} = .001$



$q_a^2 = \frac{v}{s}$ in dominance $\begin{cases} A- & 1 \\ aa & 0 \end{cases}$

$q_a = \frac{v}{s}$ in semidominance $\begin{cases} AA & s \\ Aa & 1 \\ aa & 0 \end{cases}$

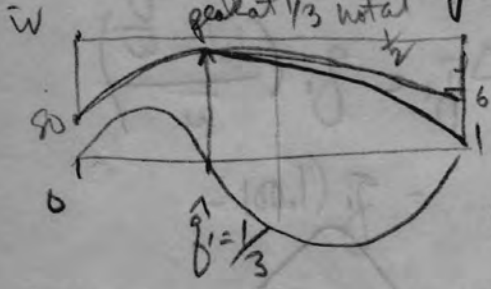
(1)

		w	
A_1A_1	q_1^2	60	$1-40$
A_1A_2	$2q_1(1-q_1)$	100	1
A_2A_2	$(1-q_1)^2$	80	$1-20$

$\frac{dw}{2dq_1} = -.40q_1 - .20(1-q_1)$

$\bar{w} = 1 - .40q_1^2 - .20(1-q_1)^2$

$\Delta q_1 = \frac{q_1(1-q_1)(-.60q_1+.20)}{1-.40q_1^2-.20q_2^2}$



$= \frac{-.60q_1(1-q_1)(q_1-\frac{1}{3})}{1-.40q_1^2-.20q_2^2} = 0$ for $\hat{q}_1$

3 solns $\hat{q}_1 = 0$ $\hat{q}_1 = 1/3$ + $\hat{q}_1 = 1$

$\bar{w}$ highest here

$\Delta q_1 = \frac{q_1(1-q_1)\sum w df}{2\bar{w}\, dq_1}$ $\sum wf = \bar{w}$ selection pressure on pop.

$= \frac{q_1(1-q_1)\left[\frac{d\bar{w}}{dq_1} - \left(\frac{d\bar{w}}{dq}\right)\right]}{2\bar{w}}$ average selection pressure on all genotypes

(33)

		$\frac{W}{2}$
A_1A_1	q_1^2	$1 + S_1 q_1$
A_1A_2	$2q_1q_2$	$1 + S_1q_1 + S_2q_2$
A_1A_3	$2q_1q_3$	$1 + S_1q_1 + S_3q_3$
A_2A_2	q_2^2	$1 + 2S_2q_2$
A_2A_3	$2q_2q_3$	$1 + S_2q_2 + S_3q_3$
A_3A_3	q_3^2	$1 + 2S_3q_3$

A_n — a low
A_{n-1} has a high selective value if q_n is high.

assumption & condition
W is a function of q proportional to q

$$\overline{W} = 1 + 2S_1q_1^3 + 2S_1q_1^2q_2 + 2S_2q_1q_2^2 + 2S_1q_1^2q_3 + 2S_3q_1q_3^2 + 2S_2q_2^3 + 2S_2q_2^2q_3 + 2S_3q_2q_3^2 + 2S_3q_3^3$$

$$= 1 + 2S_1q_1^2 + 2S_2q_2^2 + 2S_3q_3^2 = \left[1 + 2\sum S_i q_i^2\right]$$

$$W_1 = [q_1^2 + q_1q_3 + q_1q_2 + 2S_1q_1^3 + S_1q_1^2q_2 + S_2q_1q_2^2 + S_1q_1^2q_3 \times$$

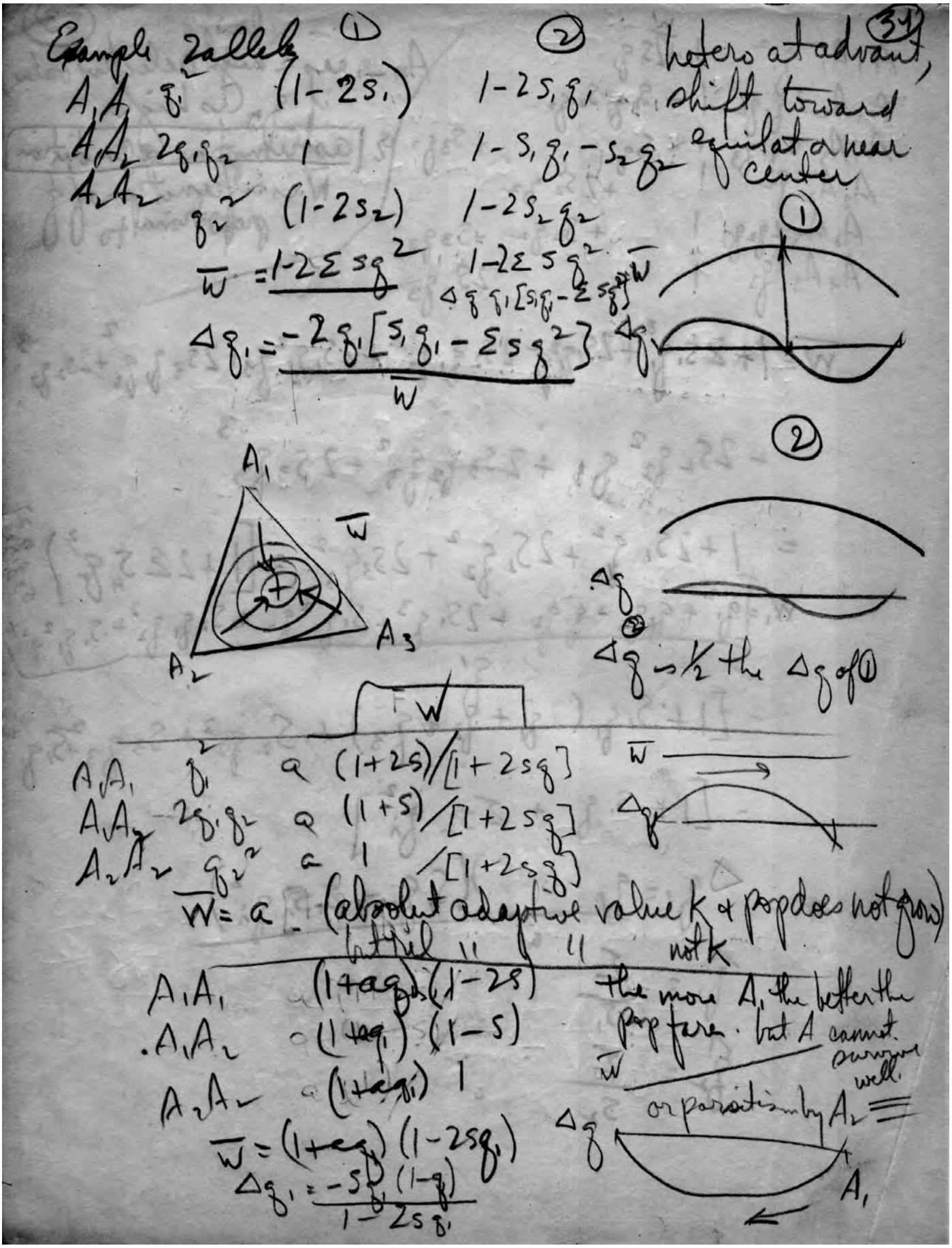
$$= [1 + S_1q_1(q_1 + q_2 + q_3) + S_2q_2^2 + S_3q_3^2 + S_1q_1^2$$

$$= [1 + S_1q_1 + \Sigma S_i q_i^2]$$

$$\Delta q_1 = \frac{q_1(S_1q_1 - \Sigma S_i q_i^2)}{\bar{w}}$$

$$\hat{q}_1 = \frac{\Sigma}{S_1}$$

$$\hat{q}_2 = \frac{\Sigma}{S_2}$$


Example 2 alleles
(1)
(2)
(34)
heters at advant, shift toward equilat a near center
A_1A_1 q^2 $(1-2s_1)$ $1-2s_1q_1$
A_1A_2 $2q_1q_2$ 1 $1-s_1q_1-s_2q_2$
A_2A_2 q_2^2 $(1-2s_2)$ $1-2s_2q_2$
$\bar{w} = 1-2\Sigma sq^2$ $1-2\Sigma sq^2$
$\Delta q_1 = \frac{-2q_1[s_1q_1 - \Sigma sq^2]}{\bar{w}}$
$\Delta q_1 = q_1[s_1q_1 - \Sigma sq^2]\bar{w}$
A_1
A_2
A_3
$\bar{w}$
Δq
Δq = ½ the Δq of (1)
A_1A_1 q_1^2 a $(1+2s)/[1+2sq]$
A_1A_2 $2q_1q_2$ a $(1+s)/[1+2sq]$
A_2A_2 q_2^2 a $1/[1+2sq]$
$\bar{w} = a$ (absolut adaptive value k & popdoes not grow)
but if " " not k
A_1A_1 $(1+aq_1)(1-2s)$
A_1A_2 $(1+aq_1)(1-s)$
A_2A_2 $(1+aq_1)1$
$\bar{w} = (1+aq_1)(1-2sq_1)$
$\Delta q_1 = \frac{-sq_1(1-q_1)}{1-2sq_1}$
the more A_1 the better the pop fare. but A cannot survive well.
or parasitism by A_2
$\bar{w}$
Δq
A_1

(35)

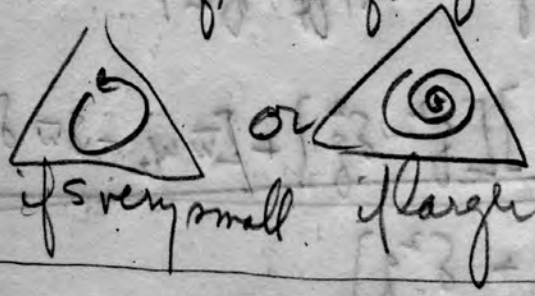
$W_{11} = a[1 + 2s(q_2 - q_3)]$ $W_{12} = a[1 + s(q_2 - q_1)]$

$W_{22} = a[1 + 2s(q_3 - q_1)]$ $W_{13} = a[1 + s(q_1 - q_3)]$

$W_{33} = a[1 + 2s(q_1 - q_2)]$ $W_{23} = a[1 + s(q_3 - q_2)]$

$\bar{W}$

$\Delta q_1 = s q_1 (q_2 - q_3)$ $\bar{W} = a$



if s very small or large on flat W plane

Monday 23 July '51

Intrabrood Selection $\bar{w} = 1$ shift in gene freq at $\bar{w} = k$

A_1A_1

A_2A_1 minor

A_2A_2 adaptive diff between brood mates

$$\Delta q = q_1(1-q_1)\left\{\left[\frac{W_{22} - W_{12}}{W_{22} + W_{12}}\right] q^2 + \left[\frac{W_{22} - W_{11}}{W_{22} + 2W_{12} + W_{11}}\right] 2q_1(1-q_1) + \left[\frac{W_{12} - W_{11}}{W_{12} + W_{11}}\right](1-q_1)^2\right\}$$

from Haldane 1930 $[(1-q_1)A_2 + q_1 A_1]$ weight

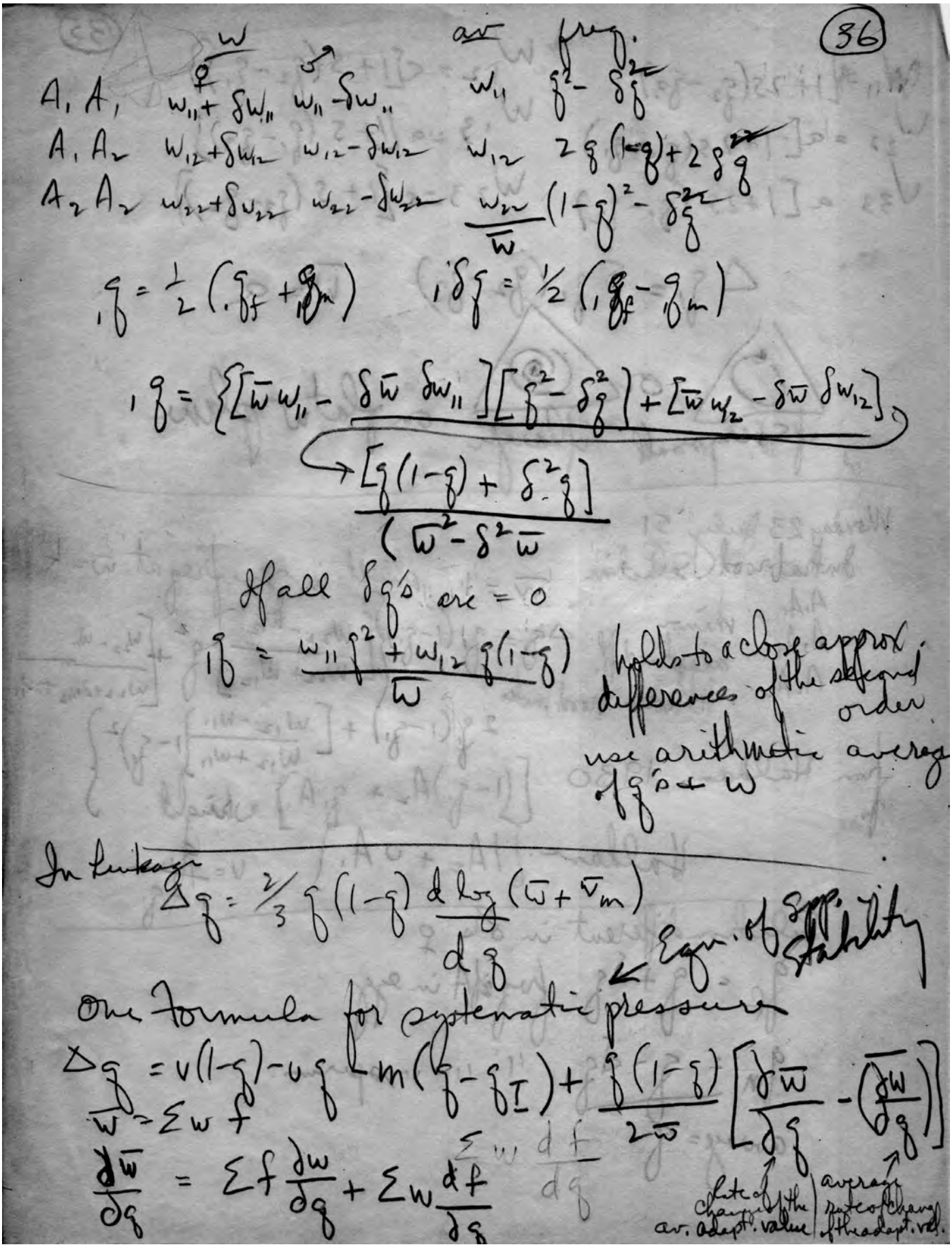
Haldane $[1A_2 + vA_1]$ $v = \frac{q_1}{1-q_1}$

Selection different in δ + φ

$q_f = q + \delta q$ freq of A in eggs

$q_m = q - \delta q$ " " " sperm.

average $= q$


(36)
w
aa
freq.
A1A1 w11+δw11 w11−δw11 w11 q²−δq²
A1A2 w12+δw12 w12−δw12 w12 2q(1−q)+2δq²
A2A2 w22+δw22 w22−δw22 w22/w̄ (1−q)²−δq²
1q = ½(1qf + 1qm)
1δq = ½(1qf − 1qm)
1q = {[w̄w11 − δw̄ δw11][q² − δq²] + [w̄w12 − δw̄ δw12]}
[q(1−q) + δ²q]
(w̄² − δ²w̄
If all δq's are = 0
1q = (w11q² + w12q(1−q))/w̄
holds to a close approx. differences of the second order
use arithmetic averag of q's & w
In linkage
Δq = ⅔q(1−q) d log(w̄ + v̄m)/dq
Eqn. of Stability
One formula for systematic pressure
Δq = v(1−q) − uq [m(q − qI) + q(1−q)/2w̄ [∂w̄/∂q − (∂w/∂q)]]
w̄ = Σwf
∂w̄/∂q = Σf ∂w/∂q + Σw df/dq
Σw df/dq
rate of change of the av. adapt. value
average rate of change of the adapt. val.

(38) (39)

Δq tends to approach 0 for all q

Random Fluctuations.
Negligible in a large random breeding population.

Unique Processes

fixation dependent on $\frac{1}{2N}$, rate of fixation/generation in population size N, rate steady state reached.
for small N use $\frac{1}{2N+1}$ (still an approx)

AA 1+2s
Aa 1+s
aa 1

a selective advantage of s for a mutant gene A may not insure fixation in a pop. fixed for aa. The random fluctuations at the ends (low freq) may tend to eliminate it.
chance of fixation here is about 2s irrespective of pop. size (Haldane) actually

$\frac{2s}{e^{4Ns}-1}$ (deleterious)

$\frac{2s}{1-e^{-4Ns}}$ (advantageous)

0 ——— 1

$\frac{1}{2N}$ non advantageous & delet.

$q_A=1$ $P=(1-2s)^{2NVt}$ ← rate/representative (as used before)

(Probability of loss of all mut. during t at rate v)

$P=\frac{1}{2}$ chosen as critical point.

$e^{-4Nsvt}=1/2$ ($e^{-x}=(1-x)$ for small x)

$4Nsvt=.69$

$v=\frac{.7}{4Nst}$

Continued (38)

Ex. $V = \frac{.7}{4 \cdot 10^{10}\ 10^{-2}\ 10^{4}} = 1.7 \times 10^{-13}$

n s t

dividing line between recurrent & non recurrent.

for large species only very small mut rate can be classed as unique.

Favorable recessive mutation

chance of fixation is $\sqrt{\frac{s}{2N}}$ (Haldane)

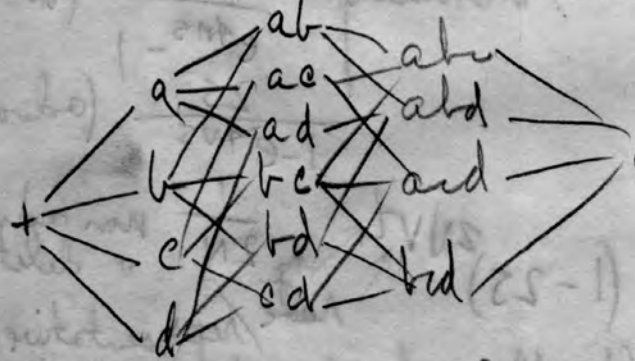
AA 1
Aa 1 $P = \left[1 - \sqrt{\frac{s}{2N}}\right]^{2Nvt} = 1/2$
aa 1+s

$e^{-\sqrt{2Ns}\, vt} = 1/2$

$\sqrt{2Ns}\, vt = .7$

$V = \frac{.7}{\sqrt{2Ns}\, t}$

$V = 10^{-8}$
using same fig as before $N = 10^{10}$
$s\ 10^{-2}$
$t\ 10^{9}$ gen



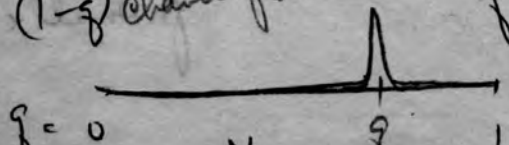
1-4s 1-s 1 1-s 1-4s

If process is slow enough then spp. will keep up with shifting peaks in $\bar{w}$ surface.

(a peak is a harmonious combination of genes.)

$(1-q)^{2N}$ chance of $\bar{a}$

q^{2N} chance of A



with a random sample of 2N gametes from a particular pop. of N

$[(1-q)a + qA]^{2N}$ array for each gene of living into next generation

(39)

q of next generation is close to that of q

$$\sigma^2_{\delta q} = \frac{q(1-q)}{2N}$$

$\rightarrow \Delta q \leftarrow$

array of possible populations for 2nd generation

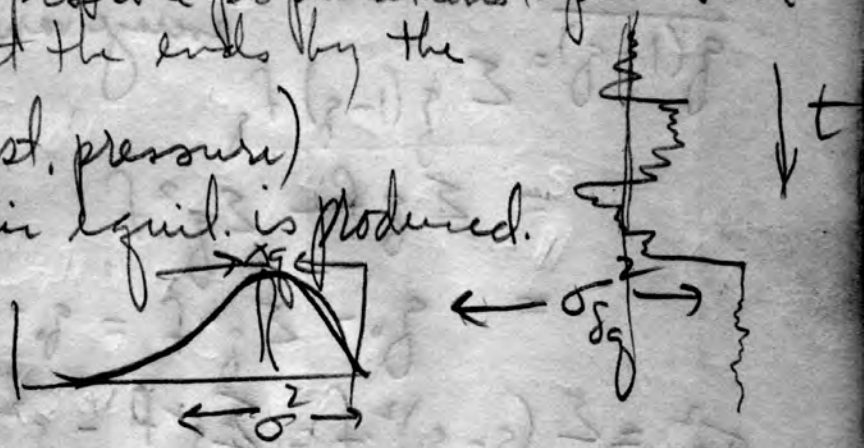
$$\sigma^2_{\delta q_2} \cong \sigma^2_{\delta q_1} + \sigma^2_{\delta q_1}$$

$$\sigma^2_{\delta q_n} = n\sigma^2_{\delta q}$$

variance of possible populations spreads out until damped at the ends by the

with a Δq (syst. pressure)

added & dynamic equil. is produced.



Wednesday 25 July

$[(1-q)a + qA]^{2N}$ distribution of sample of gametes from pop of size N

# of gametes to form a zygote # of zygote to maintain popn.

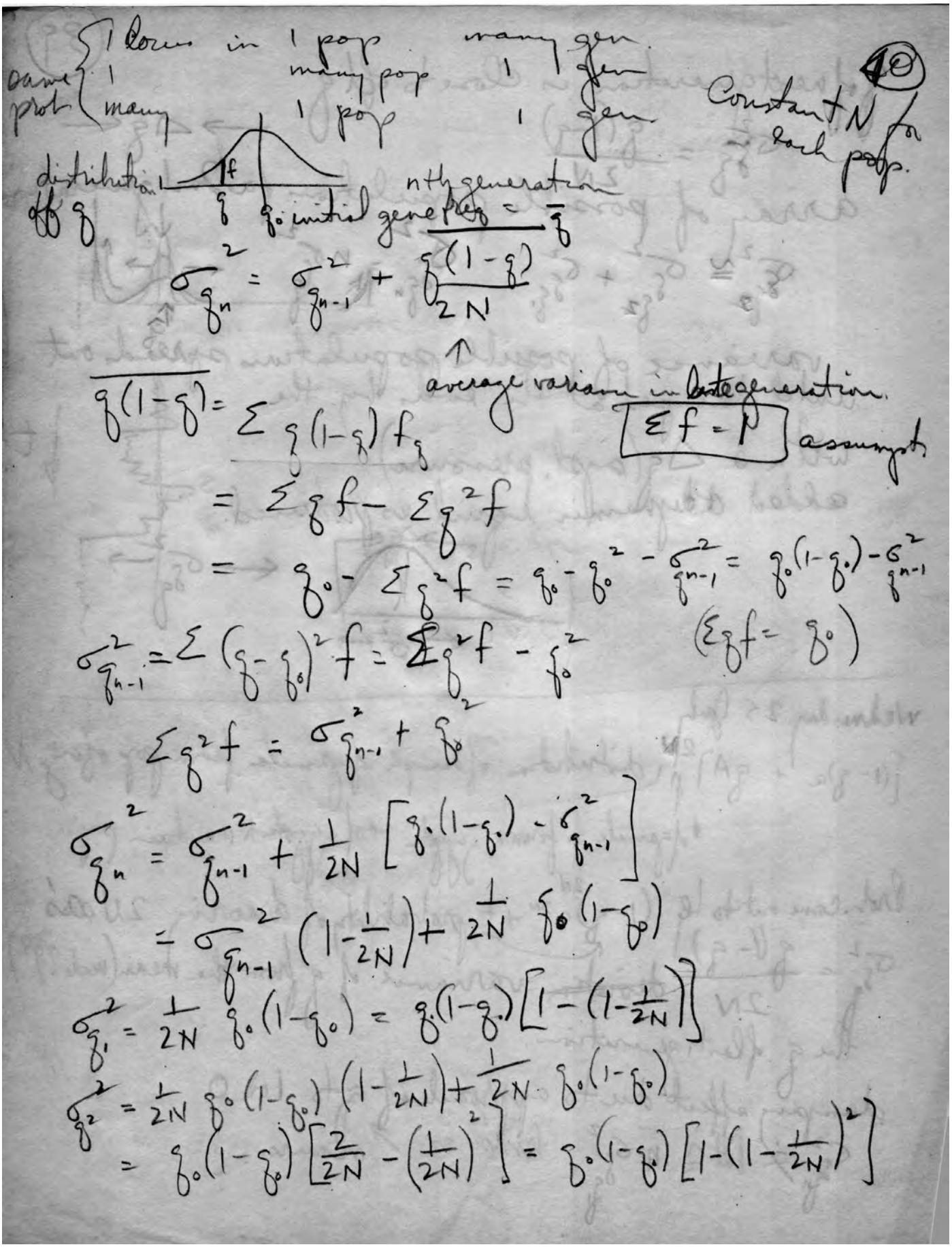
Prob. come out to be $(1-q)^{2N} a^{2N} + \ldots$ probability of drawing $2N$ as

$$\sigma^2_{\delta q} = \frac{q(1-q)}{2N}$$ ~~deviation~~ variance of q from the mean (mode ???)

the q of last generation.

damping effect due to approach of q to 1 or 0

$\sigma^2_{\delta q_n} \neq$ but $\cong n\sigma^2_{\delta q}$ less so as $\rightarrow$ occurs.


1 locus in 1 pop many gen
same 1 many pop 1 gen
prob many 1 pop 1 gen
Constant N for each pop.
distribution of q
f
q
q0 initial gene freq
nth generation
$\bar{q} = \bar{q}$
$\sigma^2_{q_n} = \sigma^2_{q_{n-1}} + \frac{\bar{q}(1-\bar{q})}{2N}$
average variance in last generation
$\overline{q(1-q)} = \sum q(1-q) f_q$
$\sum f = 1$ assumption
$= \sum qf - \sum q^2 f$
$= \bar{q}_0 - \sum q^2 f = q_0 - q_0^2 - \sigma^2_{q_{n-1}} = q_0(1-q_0) - \sigma^2_{q_{n-1}}$
$\sigma^2_{q_{n-1}} = \sum (q - q_0)^2 f = \sum q^2 f - q_0^2$ $(\sum qf = q_0)$
$\sum q^2 f = \sigma^2_{q_{n-1}} + q_0^2$
$\sigma^2_{q_n} = \sigma^2_{q_{n-1}} + \frac{1}{2N}\left[q_0(1-q_0) - \sigma^2_{q_{n-1}}\right]$
$= \sigma^2_{q_{n-1}}\left(1 - \frac{1}{2N}\right) + \frac{1}{2N} q_0(1-q_0)$
$\sigma^2_{q_1} = \frac{1}{2N} q_0(1-q_0) = q_0(1-q_0)\left[1 - \left(1 - \frac{1}{2N}\right)\right]$
$\sigma^2_{q_2} = \frac{1}{2N} q_0(1-q_0)\left(1 - \frac{1}{2N}\right) + \frac{1}{2N} q_0(1-q_0)$
$= q_0(1-q_0)\left[\frac{2}{2N} - \left(\frac{1}{2N}\right)^2\right] = q_0(1-q_0)\left[1 - \left(1 - \frac{1}{2N}\right)^2\right]$

(41)

If $\sigma^2_{q_{n-1}} = q_0(1-q_0)\left[1-\left(1-\frac{1}{2N}\right)^{n-1}\right]$

$\sigma^2_{q_n} = q_0(1-q_0)\left[1-\frac{1}{2N}-\left(1-\frac{1}{2N}\right)^{n}\right]+\frac{1}{2N}q_0(1-q_0)$

$= q_0(1-q_0)\left[1-\left(1-\frac{1}{2N}\right)^{n}\right]$ proved by math. induct.

$= q_0(1-q_0)\left[n\frac{1}{2N} - \frac{n(n-1)}{\underline{2}}\left(\frac{1}{2N}\right)^2 + \cdots +\right.$

2 factorial ↑ damping term.

$[q_0(AA)+(1-q_0)aa]$

after proportion fixed at ∞ no. of generation.

× genfreq. of donor class
recipient class

$[(1-x)a + xA]^{2Nq}$

(2Nq+1) term of exp.

a term

$(1-x)^{2N}{}_a{}^{2N}A^0 + 2N(1-x)^{2N-1}{}_a{}^{2N-1}A$ 1 term.

$f_x \cdot \frac{\underline{2N}}{\underline{2Nq}\,\underline{2N-q}} x^{2Nq}(1-x)^{2N(1-q)}$ f_x contribution of class x to class q.

$\frac{\underline{2N}}{\underline{2Nq}\,\underline{2N(1-q)}} \sum x^{2Nq}(1-x)^{2N(1-q)} \cdot f_x$ all class x to q.

$\varphi x\,dx = fx$ (42)

$f_{q\,n+1} = f_q(1-K)$ (decay at rate K)

$f_q(1-K) = \dfrac{\lfloor 2N}{\lfloor 2Nq \,\lfloor 2N(1-q)}\int_0^1 x^{2Nq}(1-x)^{2N(1-q)}\varphi(x)\,dx$

$\dfrac{\varphi(q)}{2N}(1-K) =$

$dq = \frac{1}{2N}$ (minimum increment of q due to 2N gametes.)

$\varphi(q) = C$ assumption based on approach of total distribution to level curve.

$\dfrac{c}{2N}(1-K) = \dfrac{c\,\lfloor 2N}{\lfloor 2Nq \,\lfloor 2N(1-q)}\int_0^1 x^{2Nq}(1-x)^{2N(1-q)}$

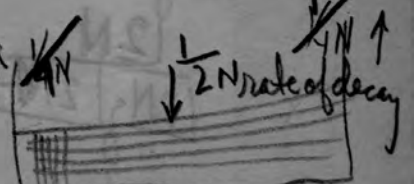
$\beta(m,n) = \int_0^1 x^{m-1}x-1^{n-1}\,dx = \dfrac{\Gamma(m)\Gamma(n)}{\Gamma(m+n)}$ ($\Gamma(n+1) = n\Gamma(n) = \lfloor n$ (for integral n)

$\dfrac{\lfloor 2N}{\lfloor 2Nq \,\lfloor 2N(1-q)}\int_0^1 = \dfrac{\Gamma(2Nq+1)\Gamma(2N(1-q)+1)}{\Gamma(2N+2)} = \dfrac{\lfloor 2Nq \,\lfloor 2N(1-q)}{\lfloor 2N+1}$

$= \dfrac{\lfloor 2N}{\lfloor 2N}\cdot 2N+1 = \dfrac{1}{2N+1}$

$1-K = \dfrac{2N}{2N+1}$ $\qquad K = \dfrac{1}{2N+1}$

(approaches a level curve as a limit)



limiting case lowering horizontally except at ends.

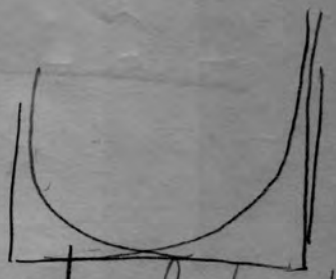
43

$\varphi(q) = \frac{c}{q} + \frac{v}{1-q}$ is a soln. If mutation occuring in both dir.

$$\frac{c}{2Nq} = \frac{(2N}{(2Nq)(2N(1-q)} \int_0^1 x^{2Nq-1}(1-x)^{2N(1-q)}\,dx$$

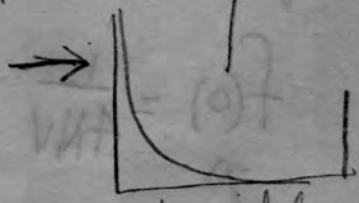
$$= \frac{\Gamma 2Nq \; \Gamma 2N(1-q)+1}{\Gamma(2N+1) \; \Gamma 2N}$$

$$\frac{c}{2Nq} = \frac{c}{2Nq}$$

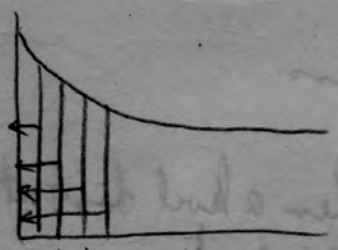


2 rectangular hyperb. represent equilibrium with mut. coming from one side only then

c & v constants such that $\int_0^1 \varphi(q)\,dq = 1$



one hyperbola. very slow rate of loss



$0, \frac{1}{2N}, \frac{2}{2N}, \frac{3}{2N}$ ... $q \rightarrow$

$e^{-1} f\frac{1}{2N}$
$e^{-2} f\frac{2}{2N}$
$e^{-3} f\frac{3}{2N}$

} group fitted by all of these classes.

Poisson dist.

$[(1-q) + qA]^n$ or $[1 - q(1-A)]^N$

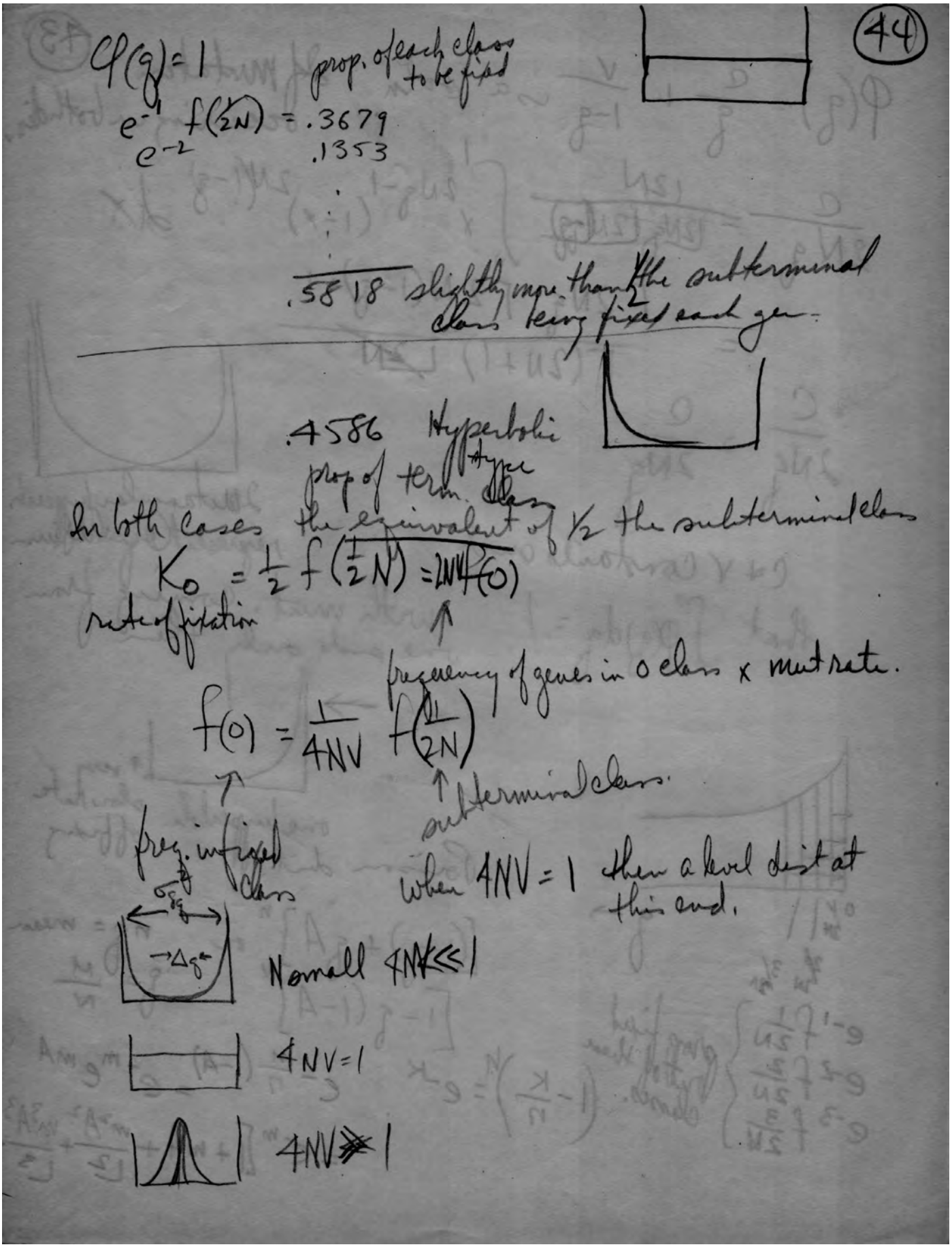
nq = mean

$q = \frac{M}{N}$

$\left(1 - \frac{K}{n}\right)^n = e^{-K}$

$e^{-\frac{m}{n}(1-A)} = e^{-m} e^{mA}$

$= e^{-m}\left[1 + mA + \frac{m^2A^2}{L^2} + \frac{m^3A^3}{L^3} \cdots\right.$


(44)
$\varphi(q) = 1$
prop. of each class to be fixed
e^{-1} $f(\frac{1}{2N})$ = .3679
e^{-2} .1353
.5818 slightly more than the subterminal class being fixed each gen.
.4586 Hyperbolic type
prop of term. class
In both cases the equivalent of ½ the subterminal class
$K_0 = \frac{1}{2} f(\frac{1}{2N}) = 2NV f(0)$
rate of fixation
frequency of genes in 0 class x mut rate.
$f(0) = \frac{1}{4NV} f(\frac{1}{2N})$
freq. in fixed class
subterminal class.
When 4NV = 1 then a level dist at this end.
$\sigma_{\Delta q}$
$\rightarrow \Delta q \leftarrow$
Normall $4NV \ll 1$
4NV=1
4NV ≫ 1

(45)

Friday July 27 1951

Distribution of gene frequency under both $\Delta_q + \sigma^2_{\delta_q}$ continued

previously considered no mutation, small rate of systematic processes

σ_{δ_q}

$q = 0$ ——— q ——— 1

$\bar{q}$

$$\varphi(q) = \frac{c}{q} + \frac{V}{1-q} = \frac{c}{q(1-q)}$$

Karl Pierson satisfying — fitting freq. dist. by first 4 moments.

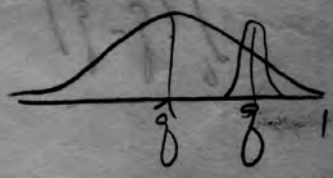
$$\mu_1 = m = \frac{\sum fv}{N} = \bar{v}$$

If moments are identical distrib. are identical

$$\mu_2 = \frac{\sum (v-\bar{v})^2 f}{N} = \sigma^2$$

$$\mu_3 = \frac{\sum (v-\bar{v})^3 f}{N} =$$ skew

$$\mu_4 = \frac{\sum (v-\bar{v})^4 f}{N} =$$ kurtosis



@ $q - \bar{q}$ in next generation.

$$\sum_{q=0}^{1} \sum_{\delta_q=-\bar{q}}^{1-\bar{q}} \left[q - \bar{q} + \delta_q + \Delta_q\right]^n f_{\delta_q} f_q = \sum_{q=\frac{1}{2N}}^{1-\frac{1}{2N}} (q-\bar{q})^n f_q$$

Equation of equilibrium

total distribution at equil.

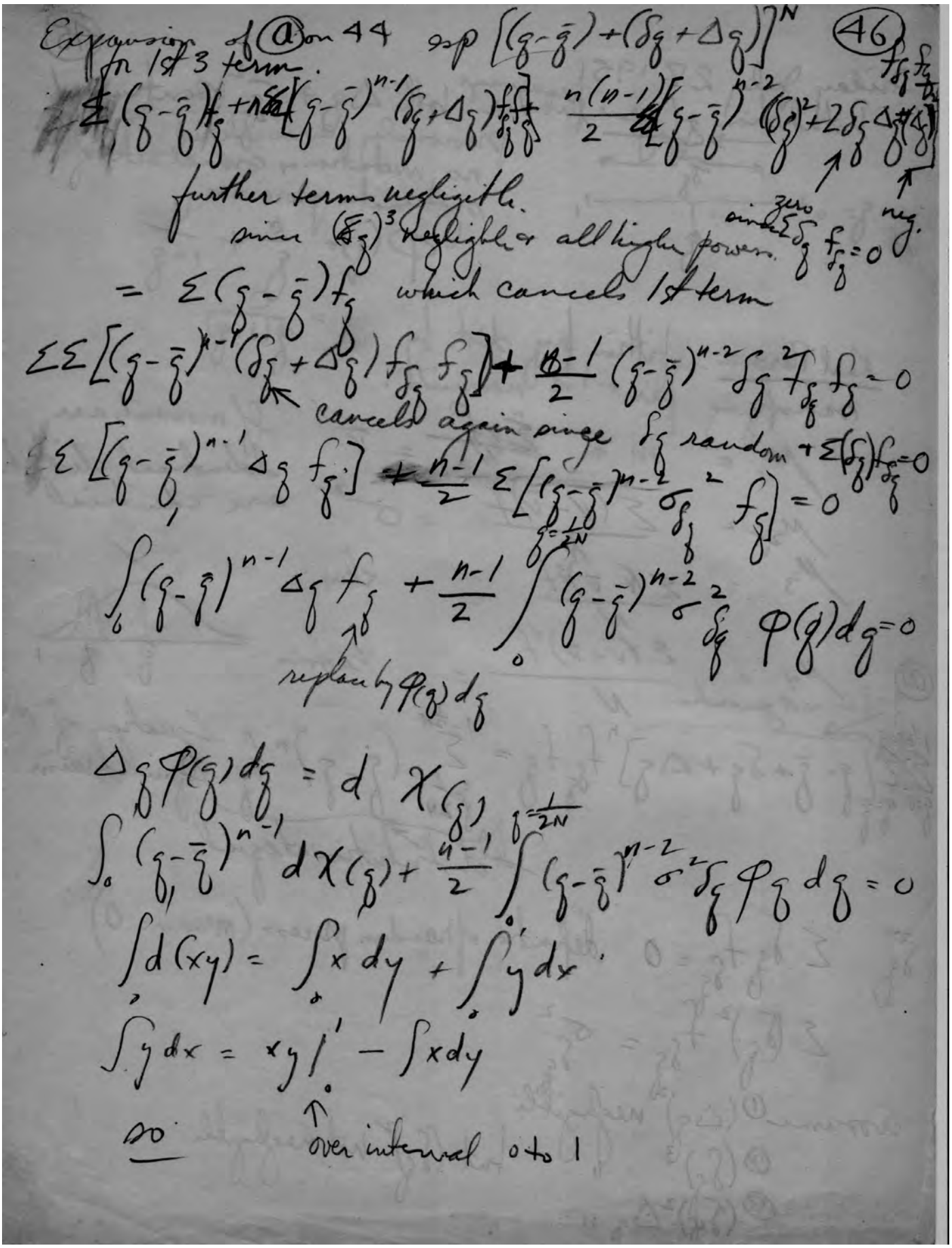
$\bar{\delta}_q$ $\sum \delta_q f_{\delta_q} = 0$ definition of random process (mean = 0)

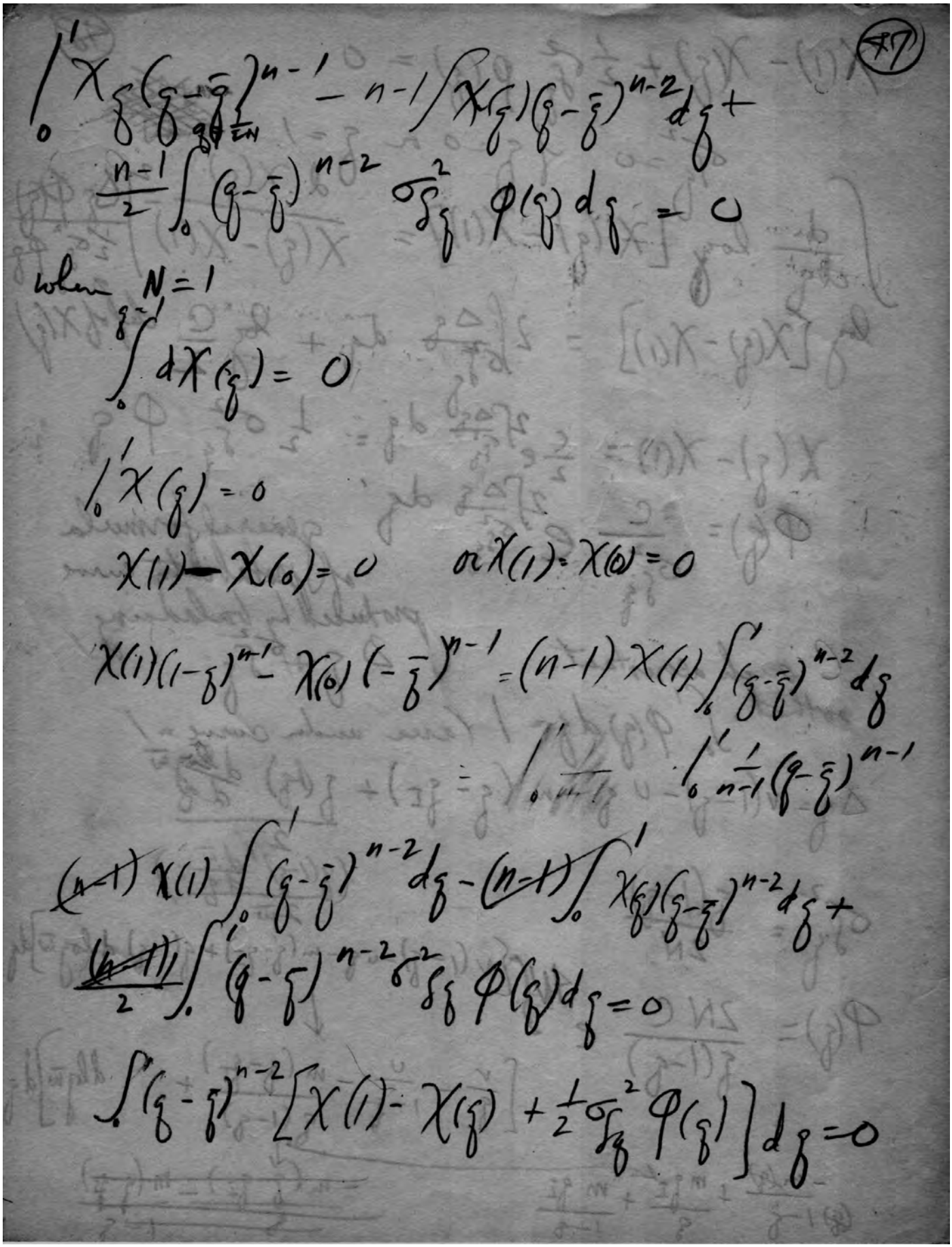
$\sum (\delta_q)^2 f_{\delta_q} = \sigma^2_{\delta_q}$

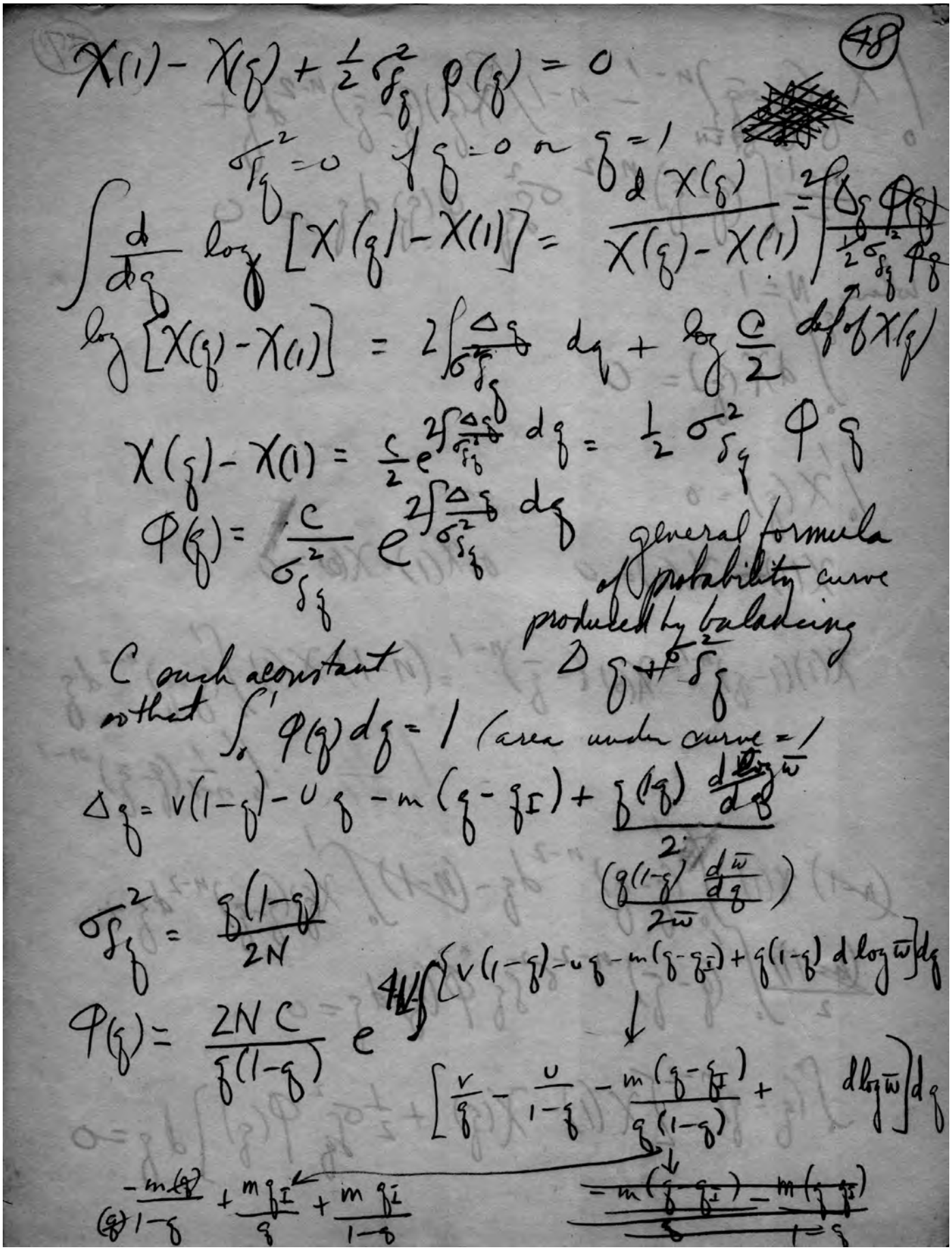
Assume ① $(\Delta_q)^2$ negligible

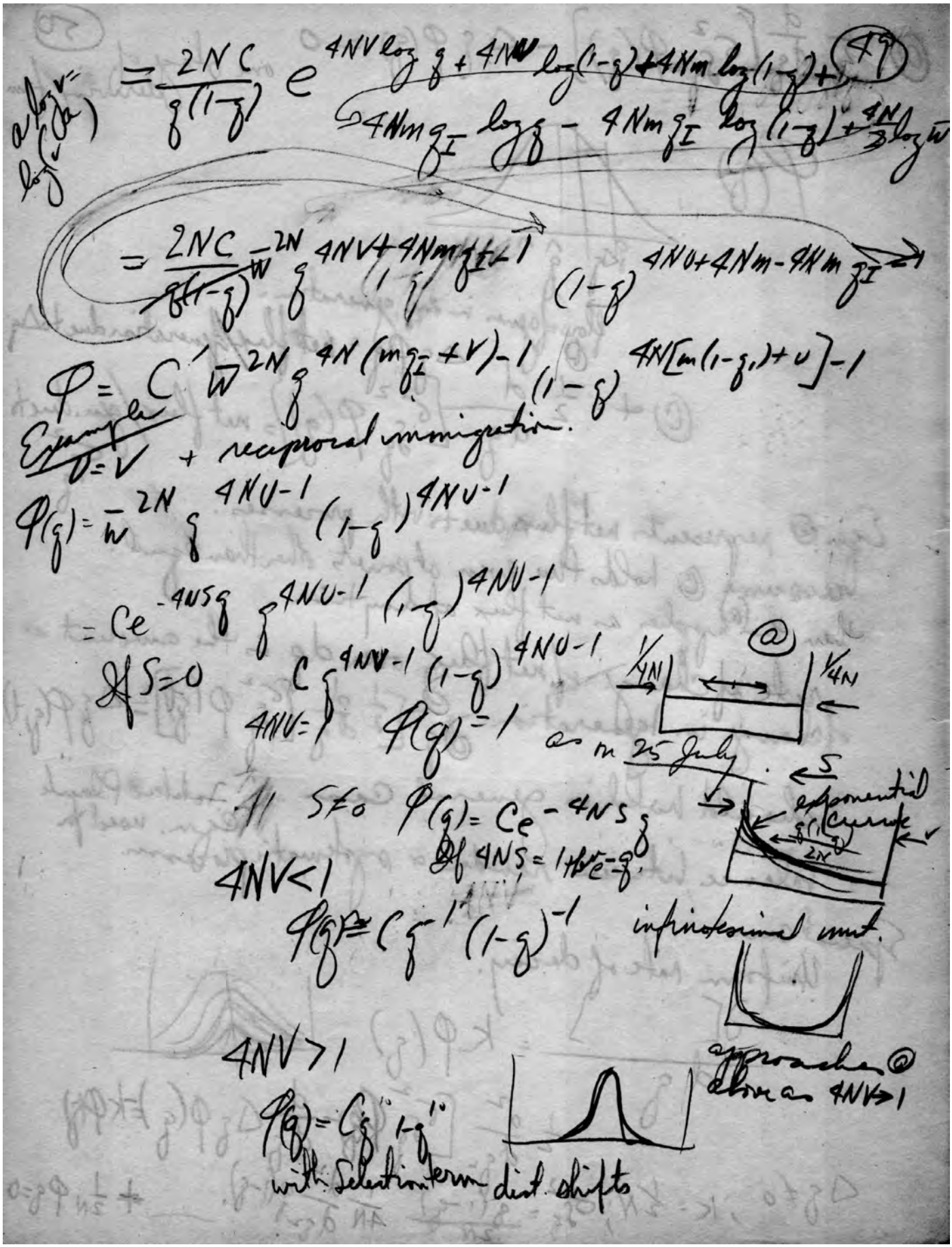
② $(\delta_q)^3$ " but $(\delta_q)^2$ not negligible.

③ $(\delta_q)^2 \Delta_q$ "


Expansion of ⓐ on 44 $\exp[(\xi-\bar{\xi})+(\delta_\xi+\Delta_\xi)]^N$ (46)
1st 3 terms.
$\sum(\xi-\bar{\xi})f_\xi + n[(\xi-\bar{\xi})^{n-1}(\delta_\xi+\Delta_\xi)f_\xi f_\xi] + \frac{n(n-1)}{2}[(\xi-\bar{\xi})^{n-2}(\delta_\xi^2+2\delta_\xi\Delta_\xi)f_\xi f_\xi]$
further terms negligible.
since $(\delta_\xi)^3$ negligible all higher powers.
zero since $\sum\delta_\xi f_\xi = 0$
neg.
$= \sum(\xi-\bar{\xi})f_\xi$ which cancels 1st term
$\sum\sum[(\xi-\bar{\xi})^{n-1}(\delta_\xi+\Delta_\xi)f_\xi f_\xi] + \frac{n-1}{2}(\xi-\bar{\xi})^{n-2}\delta_\xi^2 f_\xi f_\xi = 0$
cancels again since δ_ξ random $+\sum(\delta_\xi)f_\xi = 0$
$\sum[(\xi-\bar{\xi})^{n-1}\Delta_\xi f_\xi] + \frac{n-1}{2}\sum[(\xi-\bar{\xi})^{n-2}\sigma_\xi^2 f_\xi] = 0$
$\int_0^{\xi=\frac{1}{2N}}(\xi-\bar{\xi})^{n-1}\Delta_\xi f_\xi + \frac{n-1}{2}\int_0(\xi-\bar{\xi})^{n-2}\sigma_\xi^2\varphi(\xi)d\xi = 0$
replace by $\varphi(\xi)d\xi$
$\Delta_\xi\varphi(\xi)d\xi = d\chi(\xi)$
$\int_0^{\xi=\frac{1}{2N}}(\xi-\bar{\xi})^{n-1}d\chi(\xi) + \frac{n-1}{2}\int_0(\xi-\bar{\xi})^{n-2}\sigma_\xi^2\varphi_\xi d\xi = 0$
$\int d(xy) = \int x\,dy + \int y\,dx$
$\int y\,dx = xy\Big|_0^1 - \int x\,dy$
so
over interval 0 to 1




(48)
$X(1) - X(\xi) + \frac{1}{2}\sigma_\xi^2 \varphi(\xi) = 0$
$\sigma_{I_\xi}^2 = 0$ if $\xi = 0$ or $\xi = 1$
$\int \frac{d}{d\xi} \log_\xi [X(\xi) - X(1)] = \frac{d X(\xi)}{X(\xi) - X(1)} = \frac{2 \delta_\xi \varphi(\xi)}{\frac{1}{2}\sigma_{\delta_\xi}^2 \varphi_\xi}$
$\log [X(\xi) - X(1)] = 2\int \frac{\Delta_\xi}{\sigma_{\delta_\xi}^2} d\xi + \log \frac{C}{2}$ of $\log X(\xi)$
$X(\xi) - X(1) = \frac{C}{2} e^{2\int \frac{\Delta_\xi}{\sigma_{\delta_\xi}^2} d\xi} = \frac{1}{2}\sigma_{\delta_\xi}^2 \varphi_\xi$
$\varphi(\xi) = \frac{C}{\sigma_{\delta_\xi}^2} e^{2\int \frac{\Delta_\xi}{\sigma_{\delta_\xi}^2} d\xi}$
general formula of probability curve produced by balancing $\Delta_\xi + \sigma_{\delta_\xi}^2$
C such a constant as that $\int_0^1 \varphi(\xi) d\xi = 1$ (area under curve = 1)
$\Delta_\xi = v(1-\xi) - u\xi - m(\xi - \xi_I) + \frac{\xi(1-\xi)\frac{d\log \bar{\omega}}{d\xi}}{2}$
$\left(\frac{\xi(1-\xi)\frac{d\bar{\omega}}{d\xi}}{2\bar{\omega}}\right)$
$\sigma_{\delta_\xi}^2 = \frac{\xi(1-\xi)}{2N}$
$4N\int [v(1-\xi) - u\xi - m(\xi - \xi_I) + \xi(1-\xi) d\log \bar{\omega}] d\xi$
$\varphi(\xi) = \frac{2NC}{\xi(1-\xi)} e^{4N\int [v(1-\xi) - u\xi - m(\xi - \xi_I) + \xi(1-\xi) d\log \bar{\omega}] d\xi}$
$\left[\frac{v}{\xi} - \frac{u}{1-\xi} - \frac{m(\xi - \xi_I)}{\xi(1-\xi)} + d\log \bar{\omega}\right] d\xi$
$\frac{-m(\xi)}{(\xi)1-\xi} + \frac{m\xi_I}{\xi} + \frac{m\xi_I}{1-\xi}$
$-m(\xi - \xi_I) - m(\xi - \xi_I)$
$1 - \xi$


Example
0=V + reciprocal immigration.
If S=0
If S≠0
4NV<1
4NV>1
with Selection term dist. shifts
@ m 25 July
exponential curve
infinitesimal unit.
approaches @ above as 4NV>1

(50)

@ $+\frac{1}{2}\frac{d}{dq}\left[\sigma^2_{\Delta q}\,\varphi(q)\right] - \Delta_q \varphi(q) = 0$ one stage of deriving form

$\varphi(q)$

flow of genes in one generation.

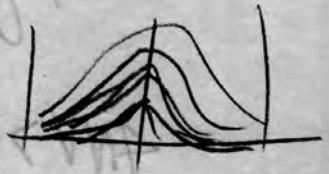
$\Delta_q \varphi_q$ = net flux/generation due to Δq

© $+\frac{1}{2}\frac{d}{dq}\left[\sigma^2_{\Delta q}\,\varphi(q)\right]$ = net flux/gen. due to $\sigma^2_{\Delta q}$.

Eqn @ represents net flux due to both processes.
assume © holds true even at points other than equil.
then this applies as net flux at any time.
rate of change of net flux over dq is the amount of change in 1 generation $\frac{d}{dq}\left[\frac{1}{2}\frac{d}{dq}\left[\sigma^2_{\Delta q}\,\varphi(q,t)\right]\right] = \Delta_q \varphi(q,t)$
should hold in general case. * Fokker Planck eqn. used for balance between random & systematic processes.

Special case
Uniform rate of decay.

$\frac{d[\quad]}{dq} = k\varphi(q)$



$\frac{1}{2}\frac{d^2}{dq^2}\left[\sigma^2_{\Delta q}\,\varphi(q)\right] - \frac{d}{dq}\Delta_q \varphi(q) = k\varphi(q)$

$\Delta q \neq 0$; $k = \frac{1}{2}N$; $\sigma^2_{\Delta q} = \frac{q(1-q)}{2N}$ $\frac{1}{4N}\frac{d^2}{dq^2}q(1-q)$ ____ $+\frac{1}{2N}\varphi q = 0$

R.A. Fisher Genetical Theory of Nat. Selection

Sumner FB 1932 Bibl. Genetica (Peromyscus)
gen. dist. + evol studies

Goldschmidt R 1933 Lymantria Bibl. Genet. XI

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White MJD 1946 Animal [redacted] in Evolution

Florkin M. 1949 Biochemical Evolution Academic Press

Romanes 1949 Adaptation

Simpson 1949 Meaning of Evolution

Allee et al Ecology

Stebbins 1950 Variation & Evolution in Plants.

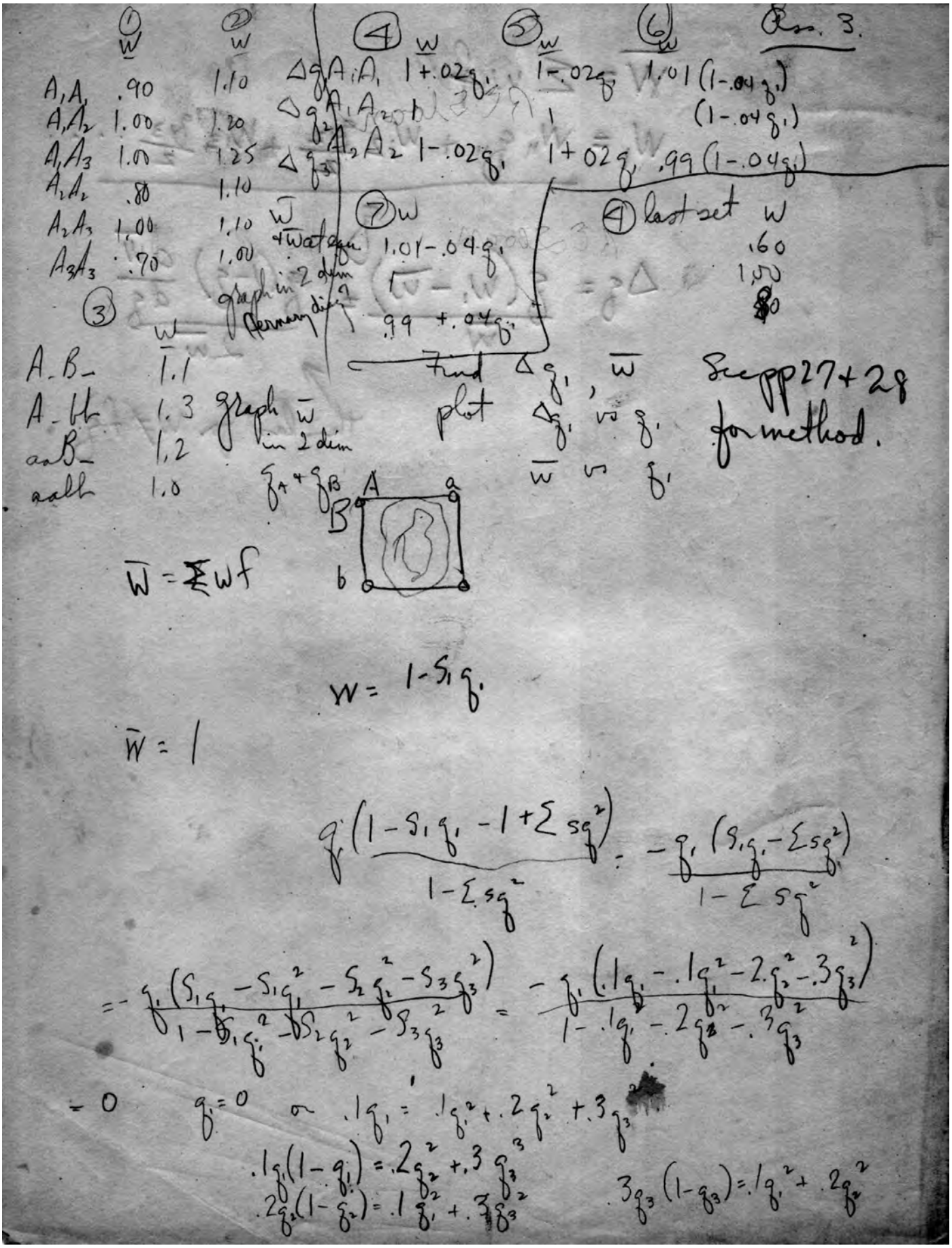
Rensch 1950

Emelianov 1949 or '50

Wright "Evolution" in Brit. (Lakst.)

} Isolated. ~10 yrs late

Choose topic by Friday
Species defin. on Mond.


Ass. 3.
A_1A_1 .90 1.10
A_1A_2 1.00 1.20
A_1A_3 1.00 1.25
A_2A_2 .80 1.10
A_2A_3 1.00 1.10
A_3A_3 .70 1.00
Δq_1 A_1A_1 $1+.02q_1$ $1-.02q_1$ $1.01(1-.04q_1)$
Δq_2 A_1A_2 1 1 $(1-.04q_1)$
Δq_3 A_2A_2 $1-.02q_1$ $1+.02q_1$ $.99(1-.04q_1)$
last set w
.60
1.00
.80
$\bar{w}-w=\Delta$
$1.01-.04q_1$
$.99+.04q_1$
find Δq_1, $\bar{w}$
plot Δq_1 vs q_1
$\bar{w}$ vs q_1
See pp 27+28 for method.
A_B_ 1.1
A_bb 1.3
aaB_ 1.2
aabb 1.0
graph $\bar{w}$ in 2 dim
q_A+q_B
A
B
a
b
$\bar{w}=\Sigma wf$
$w=1-s_1q_1$
$\bar{w}=1$
$q_1\left(\frac{1-s_1q_1-1+\Sigma sq^2}{1-\Sigma sq^2}\right)=-\frac{q_1(s_1q_1-\Sigma sq^2)}{1-\Sigma sq^2}$
$=-\frac{q_1(s_1q_1-s_1q_1^2-s_2q_2^2-s_3q_3^2)}{1-s_1q_1^2-s_2q_2^2-s_3q_3^2}=-\frac{q_1(.1q_1-.1q_1^2-.2q_2^2-.3q_3^2)}{1-.1q_1^2-.2q_2^2-.3q_3^2}$
$=0$ $q_1=0$ or $.1q_1=.1q_1^2+.2q_2^2+.3q_3^2$
$.1q_1(1-q_1)=.2q_2^2+.3q_3^2$
$.2q_2(1-q_2)=.1q_1^2+.3q_3^2$
$.3q_3(1-q_3)=.1q_1^2+.2q_2^2$

$$\bar{W} = \Sigma w f \qquad !$$

$$W_1 = W_{11} q_{11} + W_{12} \frac{q_{12}}{2} + W_{13} \frac{q_{13}}{2} \cdots$$

$$\Delta q = \frac{q(W_1 - \bar{W})}{\bar{W}} = \frac{q(1-q)\frac{d\bar{W}}{dq}}{2\bar{W}}$$

this last for $W \neq fq$

Ans to Ass. 3

A_1A_1	.90	g_1^2	$1-.1\ (S_1)$
A_1A_2	1.00	$2g_1g_2$	1
A_1A_3	1.00	$2g_1g_3$	1
A_2A_2	.80	g_2^2	$1-.2\ (S_2)$
A_2A_3	1.00	$2g_2g_3$	1
A_3A_3	.70	g_3^2	$1-.3\ (S_3)$

$\overline{W} = \Sigma w_i = 1 - \Sigma S_i g_i^2$

(51)

$W_1 = (1-S_1)g_1^2 + g_1g_2 + g_1g_3 / g_1$

$= 1 - S_1 g_1$

$W_2 = 1 - S_2 g_2$

$W_3 = 1 - S_3 g_3$

$\Delta g_1 = \frac{g_1(w-\bar{w})}{\overline{W}} = g_1\left(\frac{-S_1 g_1 + \Sigma S_i g_i^2}{\overline{W}}\right)$

similarly for $\Delta g_2 + \Delta g_3$

$S_1 g_1 = S_2 g_2 = S_3 g_3 = \Sigma S_i g_i^2$

$g_1 = \frac{1}{S_1} \Big/ \Sigma \frac{1}{S_i} = \frac{1/S_1}{\Sigma 1/S_i}$

$\hat{g}_1 = 10/\Sigma\frac{1}{S} \quad .545$

$\hat{g}_2 = 5/\Sigma\frac{1}{S} \quad .273$

$\hat{g}_3 = 10/3\Big/\Sigma\frac{1}{S} \quad .182$

$g_1 + g_2 + g_3 = 1 \quad (1-g_1-g_2)$ for g_3 (at equil)

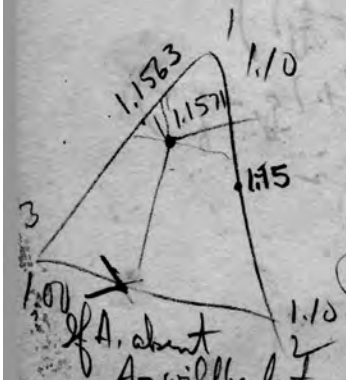
11	1.10
12	1.20
13	1.25
22	1.10
23	1.10
33	1.00

$W_1 = 1.10g_1 + 1.20g_2 + 1.25g_3 = \bar{w}$

$W_2 = 1.20g_1 + 1.18g_2 + 1.10g_3 = \bar{w}$ } dividing through in each case by the approp. g_i

$W_3 = 1.25g_1 + 1.10g_2 + 1.g_3 = \bar{w}$

$\overline{W} = 1 + .10g_1^2 + .40g_1g_2 + .50g_1g_3 + .10g_2^2 + .20g_2g_3$



① $-.15g_1 - .05g_2 + 1.25$

② $.10g_1 + 1.10$

③ $.25g_1 + .10g_2 + 1.00 = \bar{w}$

(2-1) $.25g_1 - .05g_2 = .15$ $\quad 5g_1 + 1g_2 = 3$

(3-2) $.15g_1 - .10g_2 = .10$ $\quad 3g_1 + 2g_2 = 2$

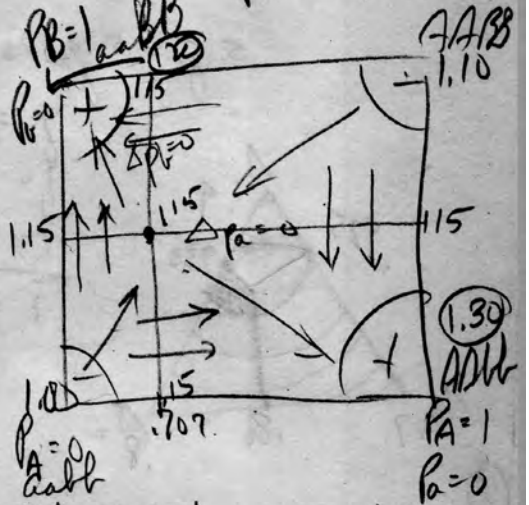
$\hat{g}_1 = \frac{4}{7} \quad \hat{g}_2 = \frac{1}{7} \quad \hat{g}_3 = \frac{2}{7}$

when w's are independent of q's the equilibrium point is the point of highest $\bar{w}$. (52)

(3) A_B_ $(1-p_a^2)(1-p_b^2)$ 1.1
A_bb $(1-p_a^2)p_b^2$ 1.3
aaB_ $p_a^2(1-p_b^2)$ 1.2
aabb $p_a^2 p_b^2$ 1.0

$\bar{w} = 1 + .1(1 - p_a^2 - p_b^2 + p_a^2 p_b^2) + .3(p_b^2 - p_a^2 p_b^2) + .2(p_a^2 - p_a^2 p_b^2)$

$= 1 + .1p_a^2 + .2p_b^2 - .4p_a^2 p_b^2$



$\frac{\partial W}{2\partial p_a} = .1p_a - .4p_a p_b^2$

$\frac{\partial W}{2\partial p_b} = .2p_b - .4p_a^2 p_b$

$\Delta p_a = \frac{.1p_a^2(1-p_a)(1-4p_b^2)}{w\,(\text{weight})} = 0$ if $p_b^2 = \frac{1}{4}$, $p_b = \frac{1}{2}$

$\Delta p_b = \frac{.2p_b^2(1-p_b)(1-2p_a^2)}{w} = 0$ if $p_a^2 = \frac{1}{2} = .707$

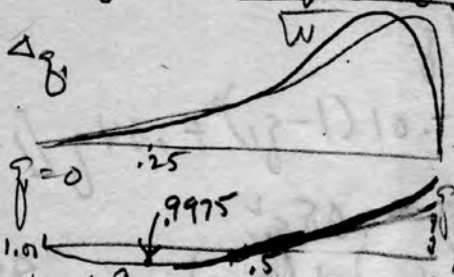
(4) A_1A_1 q_1^2 $1 + .02q_1$ $\bar{w} = 1 + .02q_1^3 - .02q_1q_2^2$
A_1A_2 $2q_1q_2$ 1 $= 1 + .02q_1(q^2 - (1-q_1)^2)$
A_2A_2 q_2^2 $1 - .02q_1$ $(q^2 - 1 + 2q_1 - q_1^2)$

$= 1 - .02q_1 + .04q_1^2$

$W_1 = (1 + .02 q_1)^2$

$\Delta q = q_1 [.02 q_1 - .02 q_1^2] = .02 q_1 (1 - q_1)$

$\frac{(W_{11} q_1^2 + W_{12} q_1 q_2)}{\bar{w}}$ Δq

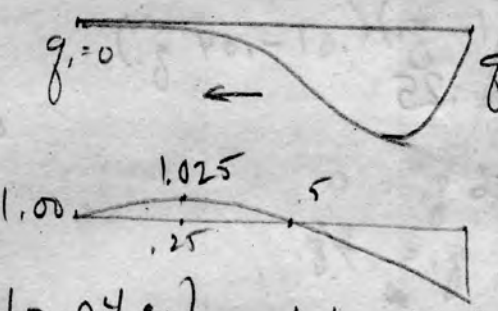


$\frac{d\bar{w}}{d q_1} = -.02 + .08 q_1 = 0$

$q_1 = .25$

(5) reversal of sign.

	$\bar{w}$
A_1A_1	$1 - .02 q_1$
A_1A_2	1
A_2A_2	$1 + .02 q_1$



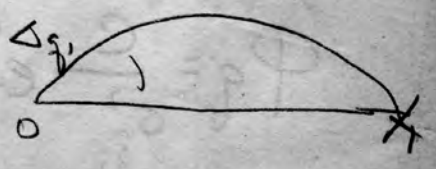
(6)

A_1A_1	$1.01 (1 - .04 q_1)$
A_1A_2	$1.01 (1 - .04 q_1)$
A_2A_2	$.99 (1 - .04 q_1)$

A_1 has high selective value but damages pop by its abundance

$\bar{w} = (1 - .04 q_1)(1 + .01 q_1 - .01 (1 - q_1)^2)$

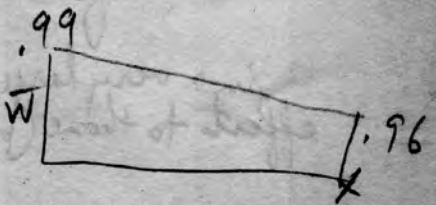
$= (1 - .04 q_1)(.99 + .02 q_1)$



$W_1 = (1 - .04 q_1)(1 + .01 q_1)$

$\Delta q_1 = \frac{q_1 [(1 - .04 q_1)(.01 - .01 q_1)}{\bar{w}}$

$\Delta q_1 = \frac{.01 q_1 (1 - q_1)(1 - .04 q_1)}{\bar{w}}$



when $\bar{w}$ is a function of q usually the adaptive peak(s) will not correspond to an $\bar{w}$.

(54)

(8) A_1A_1 $1.01-.04q_1$

A_1A_2 1

A_2A_2 $.99+.04q_1$

$\bar{W} = 1+.01q_1^2-.01(1-q_1)^2+.04q_1[1-2q_1]$

$= .99+.06q_1-.05q_1^2$

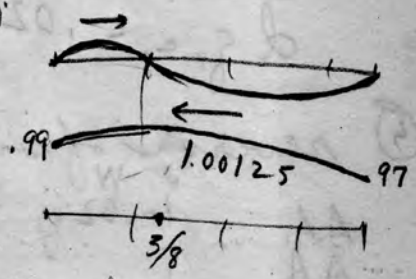
$W_1 = q_1(1.01-.04q_1)+(1-q_1)$

$= 1+.01q_1-.04q_1^2$

$\Delta q_1 = q_1[.01-.05q_1+.04q_1^2]/\bar{W}$

$= q_1(1-q_1)(.01-.04q_1)$

$\hat{q}_1 = .25$



rough correspondence of $\Delta q = 0$ + $\frac{d\bar{w}}{dq} = 0$

$\frac{d\bar{w}}{dq}$ $.06-.16q_1 = 0$

$q_1 = 3/8$

and qus. to #3

varying selection pressure

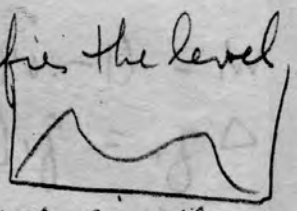
$s = \bar{s} \pm \sigma_s$

$\sigma_{\Delta q} = \sigma_s q(1-q)$

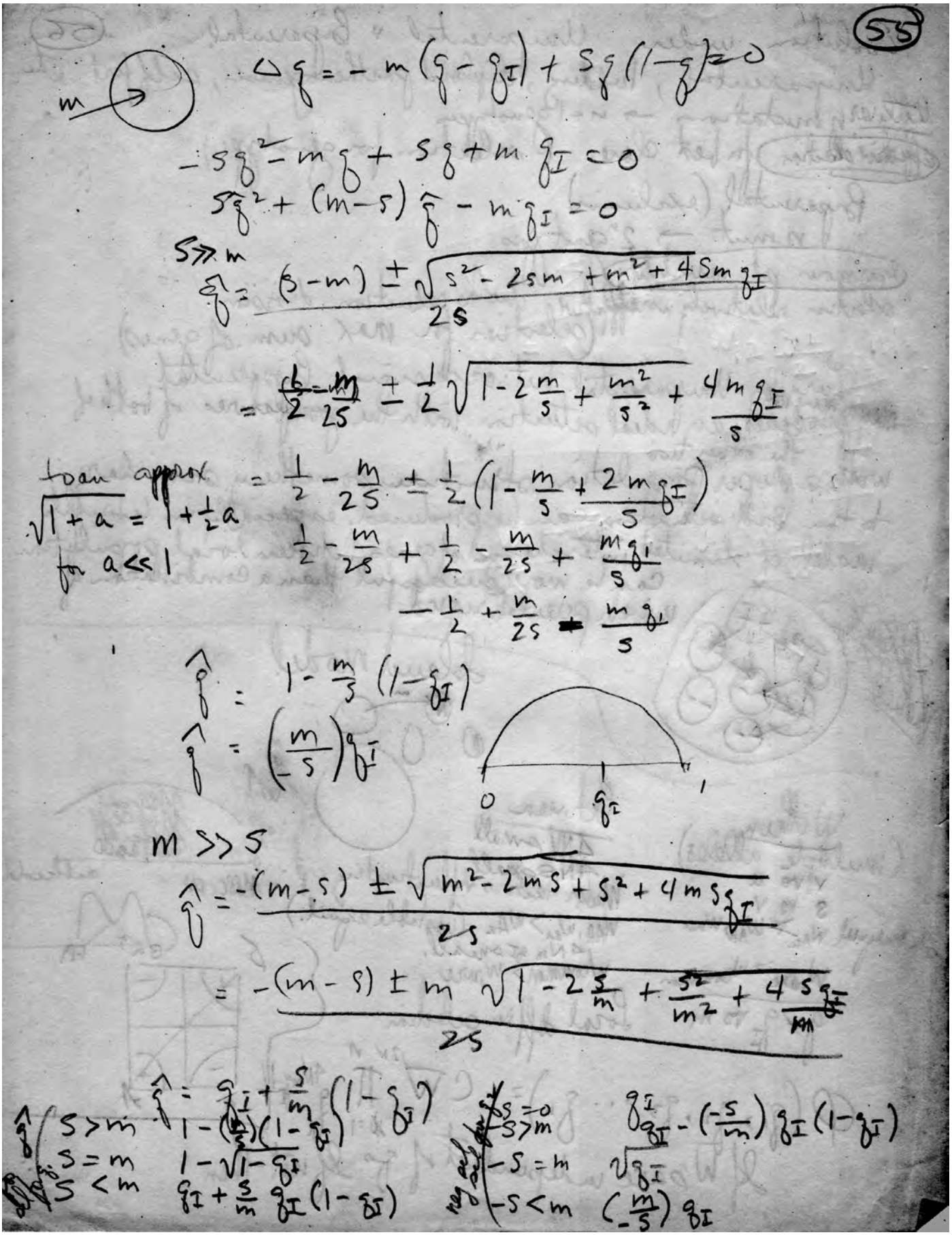
$\sigma^2_{\Delta q} = \sigma_s^2 q^2(1-q)^2$ as compared to $\sigma^2_{\Delta q} = \frac{q(1-q)}{2N}$ for const. s

$$\varphi_q = \frac{C}{\sigma^2_{\Delta q}} e^{2\int \frac{\Delta q}{\sigma^2_{\Delta q}} dq}$$

this modifies the level line to



in a very large population this will produce similar effects to those of the random element in small popns.


55
m
$\Delta \xi = -m(\xi - \xi_I) + S\xi(1-\xi) = 0$
$-S\xi^2 - m\xi + S\xi + m\xi_I = 0$
$S\xi^2 + (m-S)\hat{\xi} - m\xi_I = 0$
$S \gg m$
$\hat{\xi} = \frac{(S-m) \pm \sqrt{S^2 - 2Sm + m^2 + 4Sm\xi_I}}{2S}$
$= \frac{S-m}{2S} \pm \frac{1}{2}\sqrt{1 - 2\frac{m}{S} + \frac{m^2}{S^2} + \frac{4m\xi_I}{S}}$
taw approx
$\sqrt{1+a} = 1 + \frac{1}{2}a$
for $a \ll 1$
$= \frac{1}{2} - \frac{m}{2S} \pm \frac{1}{2}\left(1 - \frac{m}{S} + \frac{2m\xi_I}{S}\right)$
$\frac{1}{2} - \frac{m}{2S} + \frac{1}{2} - \frac{m}{2S} + \frac{m\xi_I}{S}$
$-\frac{1}{2} + \frac{m}{2S} = \frac{m\xi_I}{S}$
$\hat{\xi} = 1 - \frac{m}{S}(1-\xi_I)$
$\hat{\xi} = \left(\frac{m}{S}\right)\xi_I$
0
ξ_I
1
$m \gg S$
$\hat{\xi} = \frac{-(m-S) \pm \sqrt{m^2 - 2mS + S^2 + 4mS\xi_I}}{2S}$
$= \frac{-(m-S) \pm m\sqrt{1 - 2\frac{S}{m} + \frac{S^2}{m^2} + \frac{4S\xi_I}{m}}}{2S}$
$\hat{\xi} = \xi_I + \frac{S}{m}(1-\xi_I)$
$S > m$ $1 - \left(\frac{S}{m}\right)(1-\xi_I)$
$S = m$ $1 - \sqrt{1-\xi_I}$
$S < m$ $\xi_I + \frac{S}{m}\xi_I(1-\xi_I)$
$S = 0$ ξ_I
$S > m$ $\xi_I - \left(\frac{S}{m}\right)\xi_I(1-\xi_I)$
$-S = m$ $\sqrt{\xi_I}$
$-S < m$ $\left(\frac{m}{S}\right)\xi_I$

Evolution under Uniparental + Biparental (56)

Uniparental, budding, diploid parthenogenesis, selffert etc.

Either n mutations → $n+1$ genotypes

effective selection on best clone. (selection for genotype)

Biparental (exclusion)

n mut → 2^n genotypes.

enormous pot. variability

selection relatively ineffective due to reduction division.

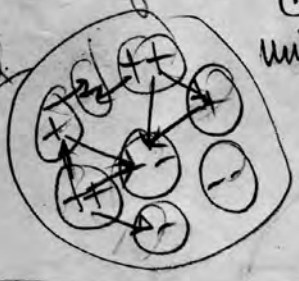
(selection for max. num. of genes)

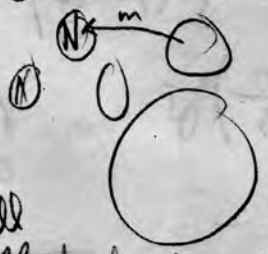
Largely Uniparental but occasional Biparental may or may not provides an ideal situation with the good features of both of the other two

with a proper population structure something similar to the Brd situation can be produced, especially in Wright model of limited interchange of genes between local population

Can be more successful than a combination of uni+bi parental reprod.

Island Model





Within (multiple alleles)

v vs u

S vs V

$W_{AA} > W_{AN} > W_{aa}$

$W_{rare} > W_{common}$

$q \neq q_I$ vs m

Between

$4Nm$ small

$4Nm$ small

Much factors ↓ fluctuating opt.

$W_{AA}, W_{aa} > W_{Aa}$ (unstable equil.)

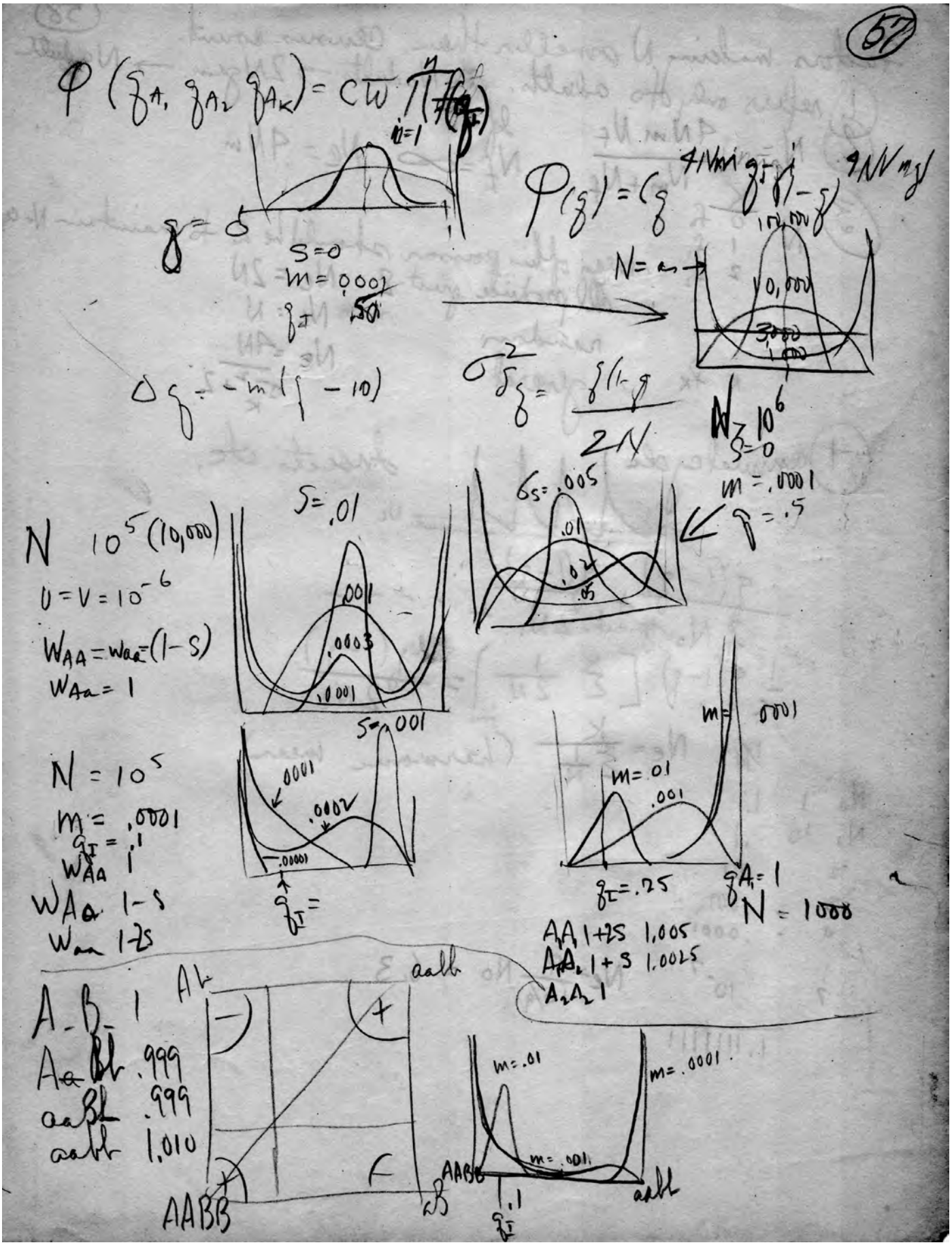
$4Nm$ ≷ equall.

$W_{common} > W_{rare}$

Local diff in selection

$$\Phi(q_1, q_2, q_3 \cdots q_n) = C W^{2N} \prod_{i=1}^{n} q_i^{4Nmq_i - 1}$$

If W are independent of q's if not then


67
$\varphi(q_{A_1}, q_{A_2} q_{A_K}) = CW \prod_{i=1}^{n} \varphi(q_i)$
$\varphi(q) = (q$
$q = \delta$
$s = 0$
$m = 0.0001$
$q_I = .5$
$N = \infty$
$\Delta q = -m(q - 10)$
$\sigma_q^2 = \frac{q(1-q)}{2N}$
$N = 10^6$
$s = 0$
$m = .0001$
$q = .5$
$s = .01$
$s = .005$
$N = 10^5 (10,000)$
$U = V = 10^{-6}$
$W_{AA} = W_{aa} = (1-s)$
$W_{Aa} = 1$
$s = .001$
$N = 10^5$
$m = .0001$
$q_I =$
W_{AA} 1
W_{Aa} 1-s
W_{aa} 1-2s
$m = .0001$
$m = .01$
$m = .001$
$q_I = .25$
$q_A = 1$
$N = 1000$
AA 1+2s 1.005
Aa 1+s 1.0025
A_2A_2 1
A_1B_1 1
A_2B_1 .999
a_2B_1 .999
a_2b_1 1.010
A_1b_1
a_2b_1
AABB
$m = .01$
$m = .0001$
$m = .001$
AABB
a_2b_1
q_I

(58)

Factors making N smaller than census count.

Nadults → 2Ngam. → Nadult

(1) refers only to adults.

(2) $N_e = \frac{4 N_m N_f}{N_m + N_f}$ If $N_f = \infty$ $N_e = 4N_m$

(3)

K	f_K
0	f_0
1	f_1
2	f_2
⋮	⋮
K	f_K

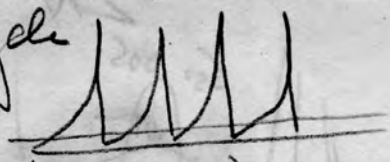
N

mean of this poisson should be 2 to maintain N = const.

all produce just 2 $N_e = 2N$

random $N_e = N$

general $N_e = \frac{4N}{\sigma_K^2 + 2}$

(4) annual cycle  Insects etc.

N_e

$$\frac{q(1-q)}{2N_0} + \frac{q(1-q)}{\text{generation } 2N_1} + \cdots$$

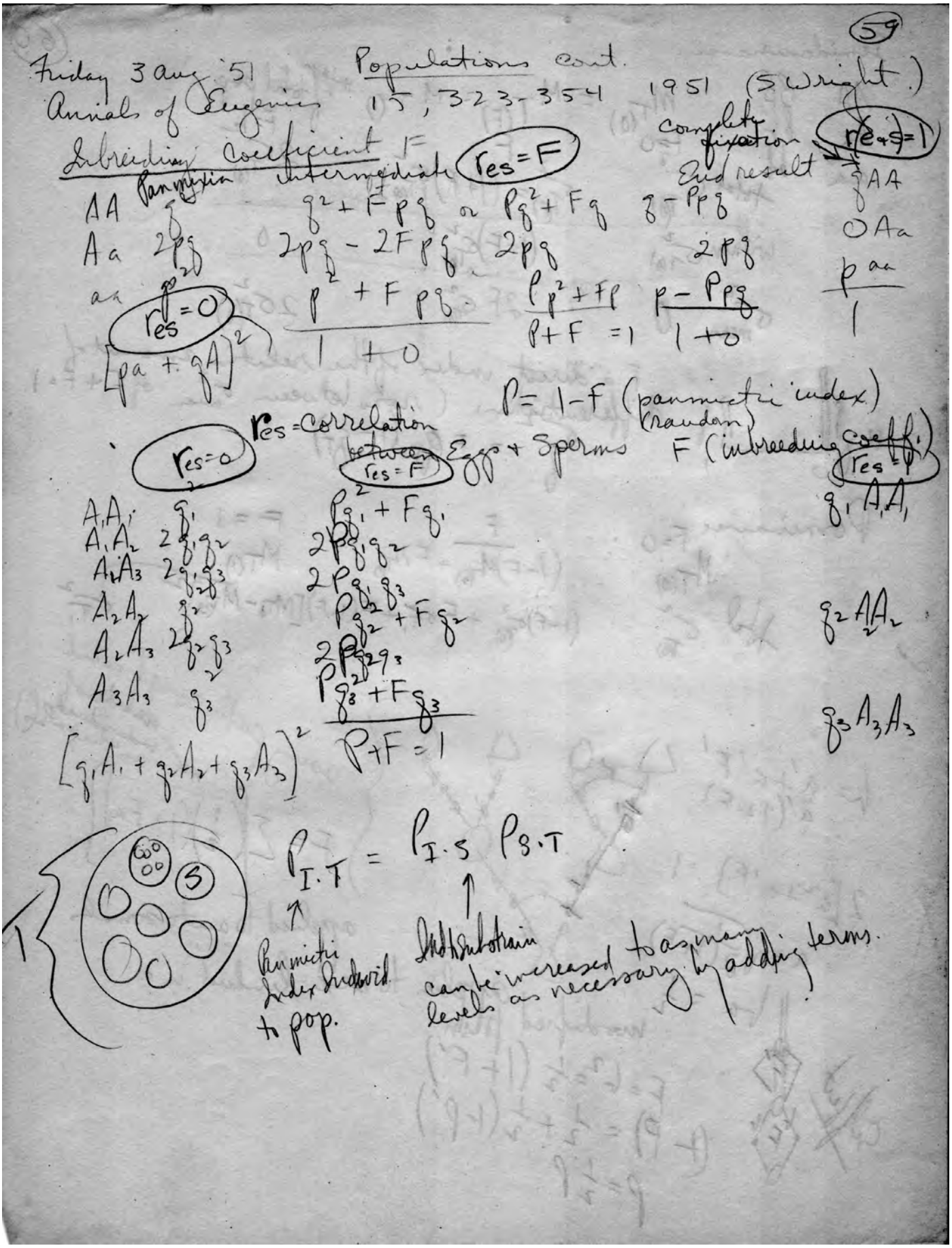
$$\frac{1}{K} q(1-q)\left[\sum^{K} \frac{1}{2N}\right] = \frac{q(1-q)}{2N_e}$$

1/N $N_e = \frac{K}{\sum \frac{1}{N}}$ (harmonic mean)

N_0	1	1.
N_1	10	.1
2		.01
3		.001
4		.0001
⋮		
7		$.10^{-7}$

$N_e = \frac{7}{10/9} N_0 = 6.3$

1.1111111


59
Friday 3 Aug '51
Annals of Eugenics
Populations cont.
15, 323-354 1951 (S Wright.)
Inbreeding coefficient F=
Panmixia
Intermediate
res=F
complete fixation
End result
res=1
AA q²
Aa 2pq
aa p²
res=0
[pa + qA]²
q² + Fpq
2pq - 2Fpq
p² + Fpq
1 + 0
or p² + Fq
2pq
p² + Fp
p + F
p - Ppq
1 + 0
q - Ppq
2pq
p - Ppq
1 + 0
AA
Aa
aa
p aa
1
p + F = 1
P = 1 - F (panmictic index)
(random)
F (inbreeding coeff.)
res = correlation between Eggs + Sperms
res=0
res=F
res=1
A1A1 q1
A1A2 2q1q2
A1A3 2q1q3
A2A2 q2²
A2A3 2q2q3
A3A3 q3²
[q1A1 + q2A2 + q3A3]²
p1² + Fq1
2pq1q2
2pq1q3
p2² + Fq2
2pq2q3
p3² + Fq3
p + F = 1
q1 A1A1
q2 A2A2
q3 A3A3
S
1
PI.T = PI.S PS.T
Panmictic index Individual + pop.
Subdivision can be increased to as many levels as necessary by adding terms.

(60)

Semidominance

	AA	Aa	aa
	BB	Bb	bb
$M_{T(0)} = M_{T(F)} = M_{T(1)}$	$F=0$	F	$F=1$
total $\sigma^2_{T(0)}$	0	$(1+F)\sigma^2_{T(0)}$	$2\sigma^2_{T(0)}$
within $\sigma^2_{T(0)}$	$(1-F)\sigma^2_{T(0)}$		0
σ^2_{mean}	0	$2F\sigma^2_{T(0)}$	$2\sigma^2_{T(0)}$

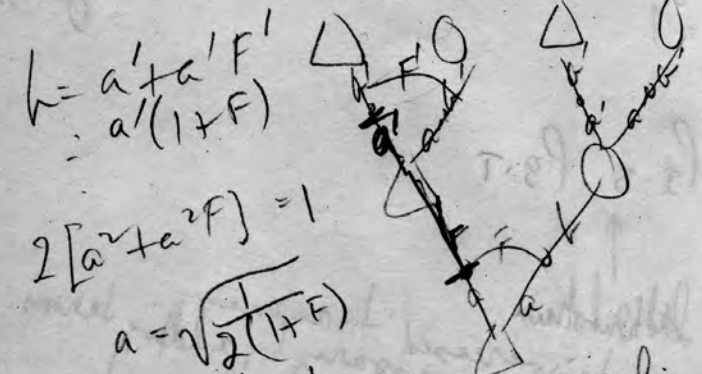
mean of total pop.

F a direct index of the relative amount of differentiation. (ratio between σ^2_{mean} of $F+F=1$

$$q = F q_T (1-q_T)$$

Dominance

	$F=0$	$\frac{F}{(1-F)M_{T(0)} + F M_{T(1)}}$	$F=1$
	$M_{T(0)}$		$M_{T(1)}$
total	$\sigma^2_{T(0)}$	$(1+F)\sigma^2_{T(0)} + F\sigma^2_{T_1} + F(1-F)[M_{T_1} - M_{T(0)}]^2$	$\sigma^2_{T_1}$



$h = a' + a'F'$

$= a'(1+F)$

$2[a^2 + a^2F] = 1$

$a = \sqrt{\frac{1}{2(1+F)}}$

$a' = \frac{1}{2}$

using path coefficient

number of individuals in the path(s)

$$F = \sum\left[\left(\frac{1}{2}\right)^n (1+F_a)\right]$$

applied to autosomals

applies to sex-linked in a modified form.

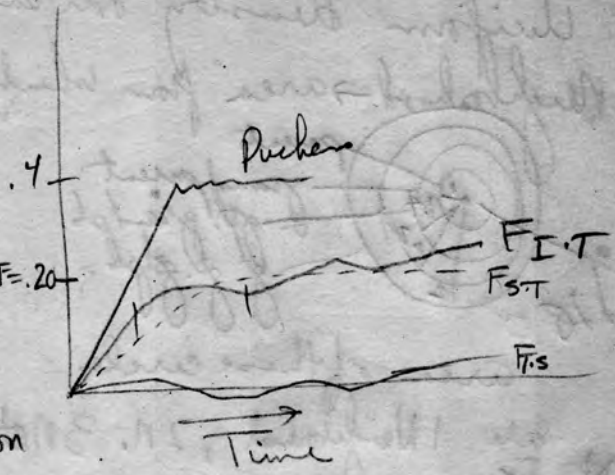
$F = h^2 = \frac{1}{2}(1+F')$

$(1+P) = \frac{1}{2} + \frac{1}{2}(1-P')$

$P = \frac{1}{2}P'$

(61)

Shorthorn cattle Durham



brother-sister mating 19.1% lost/generation

$F = (\tfrac{1}{4})^2[2F' + 2b'^2]$

$= \tfrac{1}{4}[2F' + 1 + F'']$

$1 - P = \tfrac{1}{4}[2 - 2P' + 1 + 1 - P'']$

$P = \frac{P'}{2} + \frac{P''}{4}$

$\frac{P}{P'} = \frac{P'}{P''} = \frac{P''}{P'''}$

Double 1st Cousins: $P = \frac{P''}{2} + \frac{P'''}{4} + \frac{P'''}{8}$

8% lost/generation.

N ↑ 1

prop. of all but $\frac{1}{N}b^2 + (1 - \frac{1}{N})F'$

$\frac{1}{2N}(1 + F') + (1 - \frac{1}{N})F'$

$\frac{1}{2N} + \frac{F'}{2N} + F' - \frac{F'}{N}$

$F = \frac{1}{2N} + (1 - \frac{1}{2N})F'$

$P = (1 - \frac{1}{2N})P'$

Isolation by Distance

(12)

Uniform density over large area, with little dispersion.

Neighborhood → area from which parents may be drawn at random.

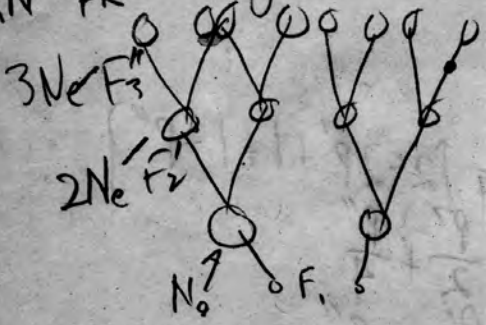
σ^2 (① w/radius 2σ) for prob. of .01

when linear $= 3.5\,\sigma_d$ (distance)

area of these circles are 1 Neighborhood, 2 N, 3 N etc.

KN: total pop

KN F_K



$$F_{1K} = \frac{1}{N}b^2 + 4\left(1-\frac{1}{N}\right)(b\alpha')^2 F_{2K}$$

$$= \frac{1}{N}\left(\frac{1+F_{11K}'}{2}\right) + \left(1-\frac{1}{N}\right)F_{21K}'$$

$$F_{2K}' = \frac{1}{2N}\left(\frac{1+F_{11K}''}{2}\right) + \left(1-\frac{1}{N}\right)F_{3K}''$$

$$F_{3K}' \; \frac{1}{3N}\left(\frac{1+F_{11K}'''}{2}\right) + \left(1-\frac{1}{N}\right)F_{4K}'$$

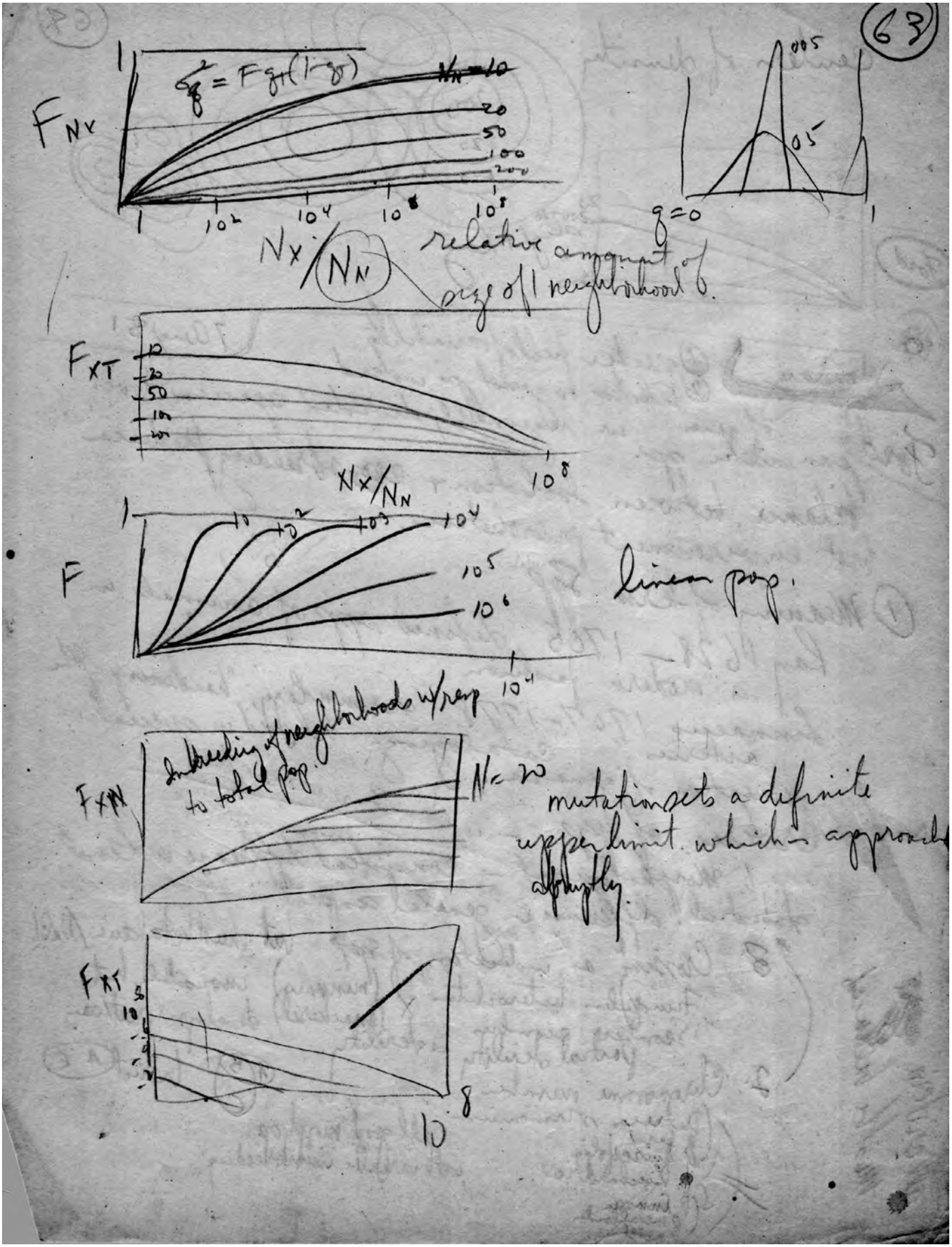
when stability reached

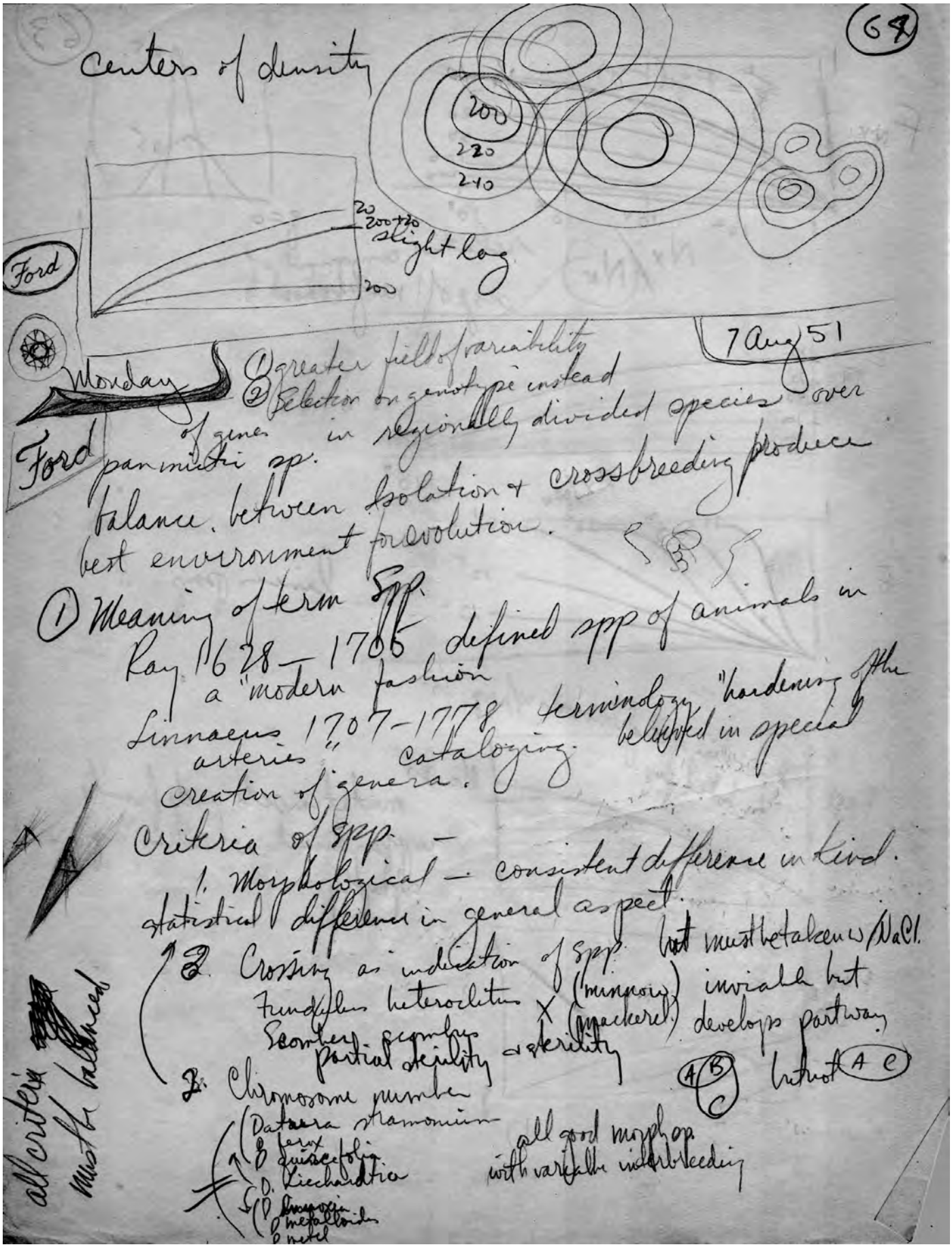
$$F_{1K} = \frac{\sum^{k-1} t_Y}{2N_1 - \Sigma t}$$

$$\Sigma t = \left[1 + \frac{1}{2}\left(1-\frac{1}{N}\right) + \frac{1}{3}\left(1-\frac{1}{N}\right)\left(1-\frac{1}{2N}\right) + \frac{1}{4}\left(1-\frac{1}{N}\right)\left(1-\frac{1}{2N}\right)\left(1-\frac{1}{3N}\right)\cdots\right.$$

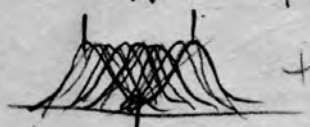
$\Sigma t \to N$ for infinite # of terms.

for finite # of terms $= \Sigma$


63
$\sigma_q^2 = Fq(1-q)$
F_{Nx}
1
20
50
100
200
10^2
10^4
10^6
10^8
N_x/N_N
relative amount of
size of 1 neighborhood
.005
.01
q=0
1
F_{XT}
10
20
50
100
10^8
N_x/N_N
F
10^2
10^3
10^4
10^5
10^6
10^7
linear pop.
Inbreeding of neighborhoods w/resp
to total pop.
F_{XN}
N= 20
mutation sets a definite
upper limit which is approached
asymptotically.
F_{XT}
5
10
8
10


64
Centers of density
200
220
240
20
200+20
slight log
200
Ford
Ford
Monday
7 Aug 51
① greater field of variability
② Selection on genotype instead
of genes in regionally divided species over
panmictic sp.
Balance between isolation & crossbreeding produces
best environment for evolution.
(1) Meaning of term Spp.
Ray 1628–1705 defined spp of animals in
a "modern fashion"
Linnaeus 1707–1778 terminology "hardening of the
arteries" cataloging. developed in special
creation of genera.
Criteria of spp. –
1. Morphological – consistent difference in kind.
statistical difference in general aspect.
2. Crossing as indication of spp. but must be taken w/ NaCl.
Fundulus heteroclitus (minnow) × (mackerel) inviable but
Scomber scombrus partial sterility & sterility develops partway
4 B C but not A C
3. Chromosome number
(Datura stramonium
D. ferox
D. quercifolia
D. Kiechardtia
D. Stramonium
D. metaloides
D. metel
all good morphological species
with variable interbreeding
all criteria
must be balanced

New concept of spp.
Little difficulty in describing spp of a region
polytypic species are the rule not the exception (Rassenkreis)



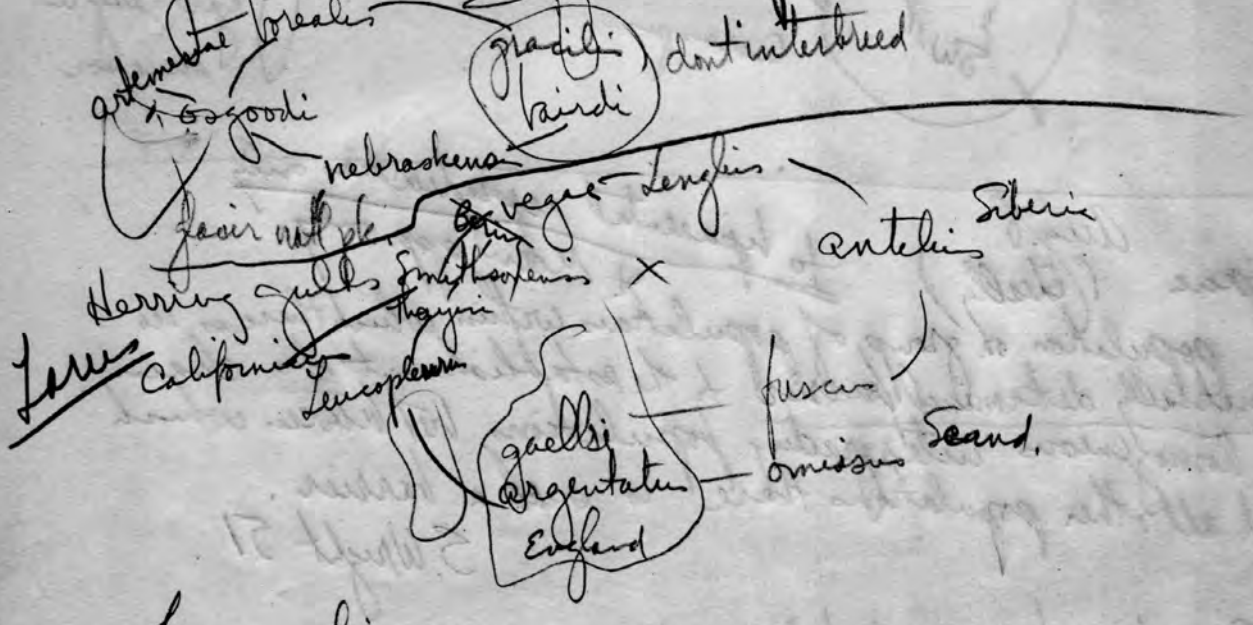
the species as a population with continuity of interbreeding
a group of spp.
A species is a population within which there is or has recently been continuity of interbreeding (a genetic continuity)
A subspecies is a local ~~variety~~ population
possibility of fusion by hybridization

Ecospecies Lab tests

Peromyscus leucopus
P gossypinus } same range, lab hybrids, no nat. hybrid.

Co-existence without hybrid forming to any great extent usually valid criterion. but rings such as.

Osgood + P. maniculatus ssp.

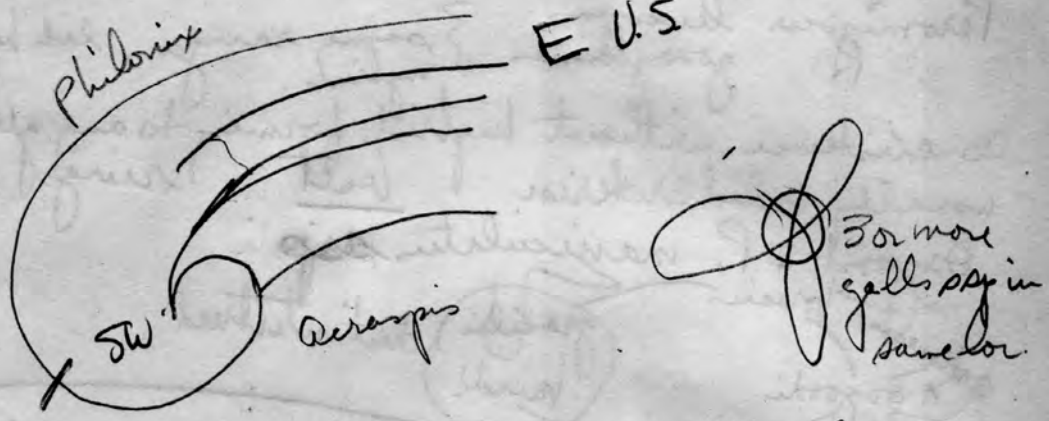


Thamnophis
Crotalus

66

Kinsey Cynips (gall wasps)

Subgenera	Complexes	Sp.
Cynips	6	11
Acritus	3	12
Besbicus	3	8
Atrusca	5	48
Philonix	2	22
Aerosapis	7	64
6	26	165
	(normal Sp?)	



Aug. 8

Species (ideally) a population or group of populations within which there is no genetically determined barrier to the establishment of a stable of homozygous intergrading populations but between which and all other populations there is such a barrier.

to biparental reproduction only
& recent spp. only.

S. Wright 51

Sympatric forms which live in the same region
Allopatric forms which live in separate regions with a geographic barrier

(67)

Drosophila pseudoobscura (Race A)
" persimilis (Race B)
Canthia tamaliana
" brachydactyla
Apodemus sylvaticus
flavicollis.

virtually identical but male sterile, non vigorous hybrids, separate in nature.
twin spp problem.

Ring problem.

Allopatric spp.
hybrid fertility not too useful since artificial hybrids more common than natural. usually restricted to morph spp

Rensch. B 1929 Das Prinzip geographischen Rassenkreise und da Problem der Artbildung. (Polytypic Sp.)

Mammals - Germany
42 are members of polytypic spp
31 monotypic
17 of the 31 are bats

Birds Paridae
107 spp
92 races
→ 20 polytypic + 26 mono.

all
192 in polytypic
43 in monotypic.

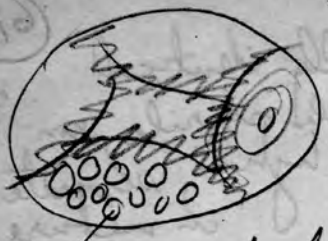
Lutra
26 spp
9 races
→ L sumatrensis maculicolli lutra platensis
in all world.

Reptiles Europe
135 poly
48 mono

Amph.
46 poly
21 mon.

Tend toward subspecies of polytypic spp universal among taxonomists of vertebrates.

(68)



Plant

Turresson } ecotype of a species partly environmental (but some selection oper.)
Clausen }

deme local population

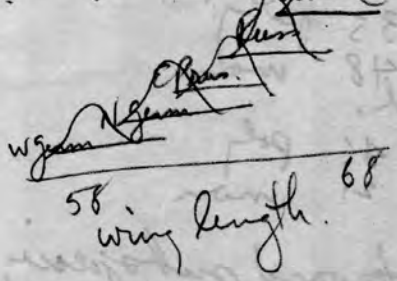
production of clones adds to trouble vegetative reproduction, apomixis.

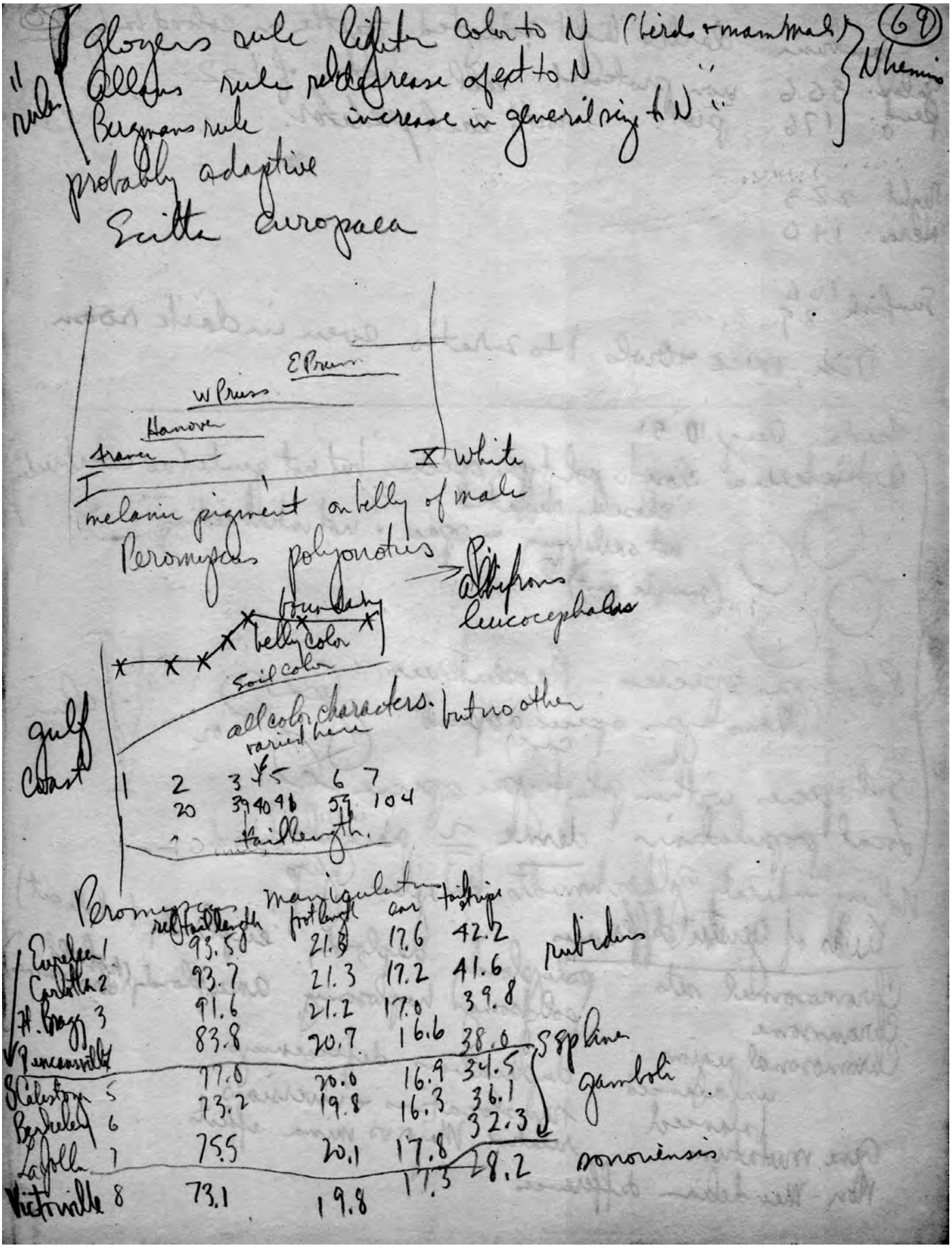
1. Bridgeless gap between ssp. + spp. (Goldschmidt.) types. Not generally taken seriously.
   No special type of difference to be regarded as specific or genetic level
2. Are diff. adaptive, nonadaptive or both
   Robson + Richards – took both views for species.
3. Is there sufficiently fine subdivision for sampling variance to play a role in evol.
4. Are subspecies incipient species.
   which more important?

Situations

Cline (Huxley)

for convenience parus atricapillus
ssp A, B, C.




Gloyers rule lighter color to N (birds + mammals)
Allens rule relative decrease of ext to N
Bergmans rule increase in general size to N
(69)
N hemis
11 rules
probably adaptive
Sciurus carolinensis
E Prussia
W Prussia
Hanover
France
X White
I
melanin pigment on belly of male
Peromyscus polionotus
albifrons
leucocephalus
boundary
belly color
soil color
all color characters but no other varied here
gulf coast
1 2 3 4 5 6 7
20 39 40 46 53 104
tail length.
Peromyscus
% tail length
manipulatus
foot length
ear length
polionotus
Eupeleo 1 93.5 21.8 17.6 42.2
Carolina 2 93.7 21.3 17.2 41.6
H. Bragg 3 91.6 21.2 17.0 39.8
Suncoosville 83.8 20.7 16.6 38.0
Galveston 5 77.0 20.0 16.9 34.5
Berkeley 6 73.2 19.8 16.3 36.1
Lapolla 7 75.5 20.1 17.8 32.3
Victorville 8 73.1 19.8 17.5 28.2
subspecies
gambeli
nebrascensis

Gambusia dark + light adapted together on colored background (20)
Galax. 866 non protected all in ratio of 1→2
Peng. 176 prot. with each predator.

Night 223
Hera. 140

Sunfish 166
79

Dice, mice + Owls 1 to 2 ratio even in dark room.

Friday Aug 10 '51

Speciation

Artenkreis close to polytypic species but not quite (no interbreeding)
closely related
not overlapping in space + not interbreeding
(may be just)

Polytypic species – Rassenkreis
(Monotypic species = special case)

or

cline

Subspecies within polytypic species
Local populations dense = neighborhood
Nothing indicate Goldschmidts hopeless

Kinds of genetic differences

Chromosomal sets — polyploidy — haploidy — euploidy (whole set)
Chromosome — polysomy — haplosomy — aneuploidy (not all chromosomes)
Chromosomal regions
unbalanced — duplications deficiencies
balanced — translocations + inversions
relative Major vs minor effects.
Gene mutations
Non-Mendelian differences

(71)

(produced from → Oenothera gigas 28 (De Vries) → " Lamarckiana 14)

Polyploidy occured in historic times in Europe. Now polyploids artificially produced by treating w/ colchicine.

50% of the Angiosperms have approximately have chromosome # differing by whole sets from other spp.

Little polyploidy in birds & mammals shrews marsupials have fewer chromosomes than placentals.

Artemia salina	21 & 42 haploid in diff var.
Solenobia pineti	30 & 60
Daphnia pulex	4 & 12
Helix pomatia	12 & 24

In forms with biparental reproduction polyploidy rare since it interferes w/ sex determining mech.

autopolyploidy from one sp.

{allopolyploidy / amphidiploidy} doubling of sterile hybrids chromosomes mixture of chromosomes of 2 spp or genera.

Jorke { Aesculus hippocastaneum → A carnea
" plavia
Horsechestnut + buckeye
bred true from start.

Digby Primula floribunda } P. kewensis sterile at first
" verticellata } progeny cutting, then become fertile.

Wing $\frac{ABCD}{ABCD} \times \frac{MNOP}{MNOP} \rightarrow ABCDMNOP$

suggested artificial production of polyploid from no pairing

which seems to explain P. kewensis 2 VII

verified by Clausen & Goodspeed on Nicotiana tabacum 12 II
" glutinosum

Cont. which produced a 36 I individual & then doubled to 36 II N. diglota. (72)

Karpechenko 1927

Raphanus sativus radish 9 II
Brassica oleracea cabbage 9 II
got polyploidy + 18 II
Raphanobrassica bred true.

Brassica campestris 20 II Turnip 10 I
" napus 36 II Swede 18 I
napocampestris 28 I

N. tabacum 24 II × sylvestris 12 II hybrid 12 II + 12 I
× tomentosa 12 II "
× Rustyi 12 II "

N. tom. × Rustyi 12 II : "same" chrom.
tom × sylvestris 24 I } diff chrom.
Rustyi sylvestris 24 I }
∴ N tabacum has one set of Tom - Rustyi chrom & one set sylvestris chrom.

Loganberry
Rubus idaeus 28 II octoploid
" raspberry 7 II
" loganbaccus 42 II double set of raspberry + idaeus

1881 Spartina alterniflora 10 × set = 70 chrom.
" stricta 6 × 54 Europe

1870 " Townsendi new niche (mudflats) in S Fr. + Eng.
sterile till 1900 after that bipartental Hyslein 18 × 126
a new + adaptive opp.

(73)

Müntzing – synthesis of a nat sp in lab.

Galeopsis pubescens 8II)
" speciosa 8II) hybrid became fertile w/ tetraploid.
" tetraploid 16II ←

Among Angiosperms
50% have ≤12 & 12 most abundant
also in mammals.
∴ amphidiploidy can't have happened too often.

Aneuploidy
related? Pomoideae 17II characteristically
Rosaceae 7II characteristically

Darlington found

hexaploid			tetraploid	
AAA	BBB	CCC	DD	EE
AAA	BBB	CCC	DD	EE
			FF	GG
			FF	GG

seven lots during red. div.
3 lots of 6 + 4 lot of 4

Deficiencys usually lethal.
Duplication may not be lethal, known in D melanogaster.
may be duplications of sections or single bands

A A'
A A'

repeat with modification introduces more genetic material.

Barr is (6 bands) dup. can be treated stat. as gene mut.

Translocations very abundant in plants

Datura stramonium 12II
laevicarpa "
metalloides "
innoxia "

Blakeley

(4) (4) 8(2)
(8) (4 4) 2(2)
(6) (4) (4) 5(2)
(8) (4) (4) 4(2)

much rare in higher animals

Inversions very large number in D. pseudoobscura & " persimilis Dobzhansky

very little difference between AD BC + ABCD
during period where it may cause semisterility AD BC + ABCD except

74

1. you can double the chromosome (autopolyploidy) or scramble them (translocation or inversion) & do little to the morphology. You may isolate or partially isolate part of the population

in Drosoph. only ♀ cross. in eggs
Lepidoptera in sperms
proportion
otherwise usually equal in
2 chrom.
N (# of ♂♂ ♀♀) that new type can be established

ADBC × ABCD
50% chance of elm sterility

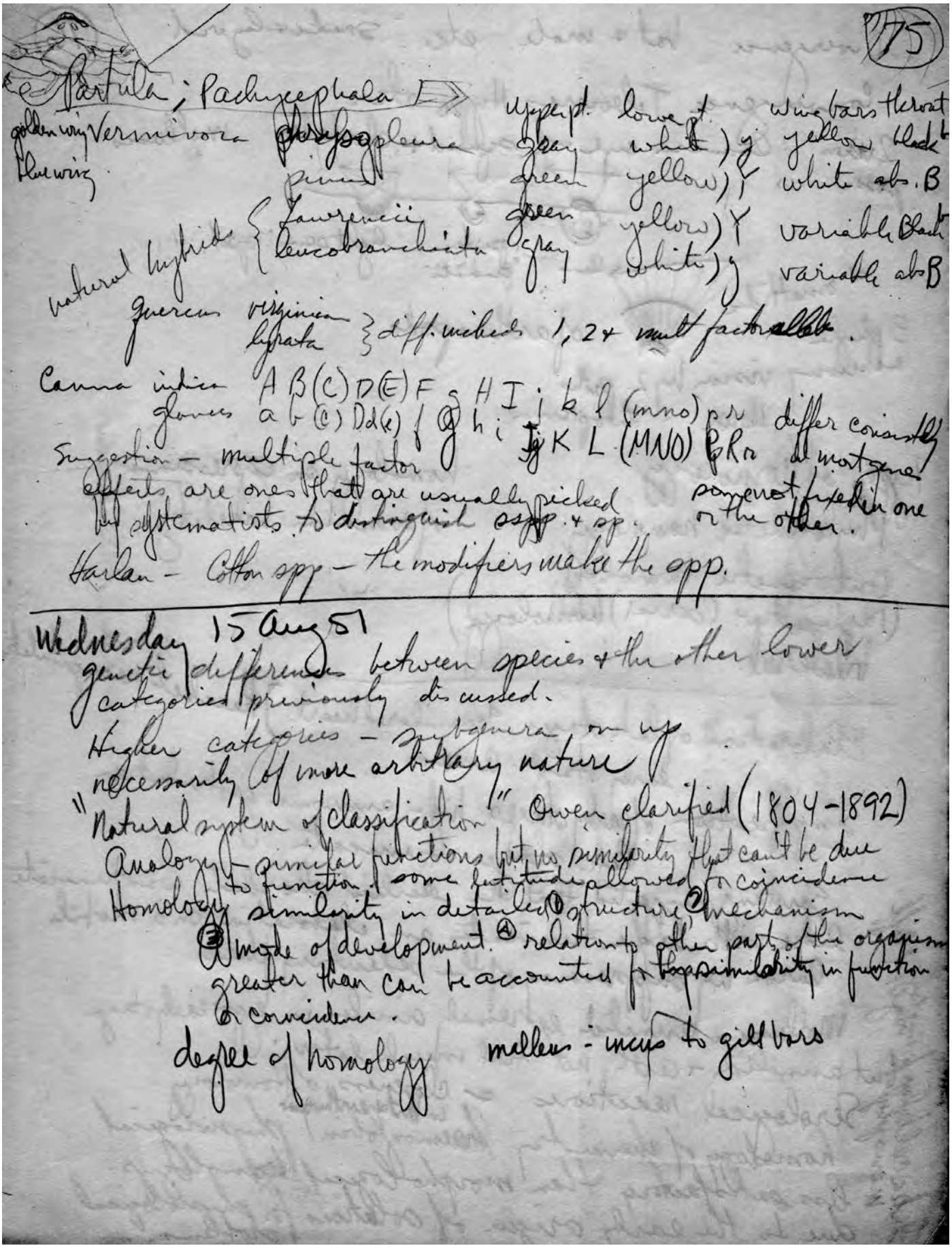
Plants	N	
	10	10^{-3}
	20	2×10^{-6}
	50	3×10^{-14}

Animals	N	
	20	3×10^{-3}
	50	4×10^{-6}
	100	3×10^{-10}
	200	5×10^{-18}

reestablishment by single ♂♀ outside region with several extinction passing through bottleneck with small N
as in Newts + Drosophila.
almost required by translocation.

Monday 13 Dec '54
spontaneous gene mutations may be quite common as heterozygote.
polymorphism — 2 or more varieties appearing in the population
striped + banded king snakes etc.
Platypoecilus melanophore patterns multiple allelic
Land Snails; Human blood groups
Inversion of D pseudoobscura (Th. Dobz.
Self incompatibility
Geographic variation in gene frequency
Blood group maps

Heterozygotes
St St } one season almost all
St Ch }
Ch Ch } the other almost all



175

Parula ; Pachycephala ⟹

		upper pt.	lower pt.	wing bars throat
golden-wing	Vermivora chrysoptera	gray	white) ½	yellow black
blue-wing	pinus	green	yellow) ½	white abs. B
natural hybrids	Lawrencii	green	yellow) ¼	variable black
	leucobronchialis	gray	white) ¼	variable abs B

Quercus virginiana / hybrata } diff. indices 1, 2+ vault factor all abb.

Canna indica A B (C) D (E) F G H I j k l (mno) p r
glauca a b (c) D d (e) f (g) h i j K L (MNO) p R r

differ consistently & most genes apparent to either one or the other.

Suggestion — multiple factor effects are ones that are usually picked by systematists to distinguish spp. & sp.

Harlan — Cotton spp — the modifiers make the spp.

Wednesday 15 Aug 51

genetic differences between species & the other lower categories previously discussed.

Higher categories — subgenera or up

necessarily of more arbitrary nature

"Natural system of classification" Owen clarified (1804-1892)

Analogy — similar functions but no similarity that can't be due to function / some latitude allowed for coincidence

Homology — similarity in detailed ① structure ② mechanism ③ mode of development ④ relation to other parts of the organism greater than can be accounted for by similarity in function & coincidence.

degree of homology

mallein - inoc to gill bars

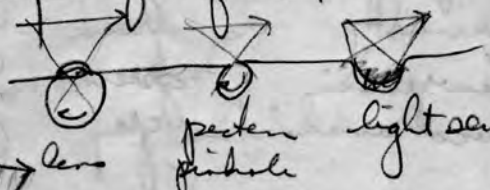
(76)

Divergence bat & mole etc. snake & lizard

Convergence Teleoceras Hippo etc.

Vision Camera eye of squid + chordates molluscs

poss.



& ommatidia

3 phyla of arthropods

achieving vision by 2 paths

Horse - Lepidoptera

Types of homology

Phylogenetic homology

Ontogenetic homology

(replicative (serial) homology)

Bilateral

homology an expression of common heredity

Elaboration of late stages 4 chambered heart. } Haeckel recapitulation

early stages Amnion

Simplification of early stages higher amnionic gastrulation

late stages truncate

Garstang suggested that the earliest chordate was truncate like with higher tunicates an elaboration on a motile larva by suppression of the sedentary phase.

Molluscs & annelids extremely similar in egg & early stages but annelid & arth. not till much later.

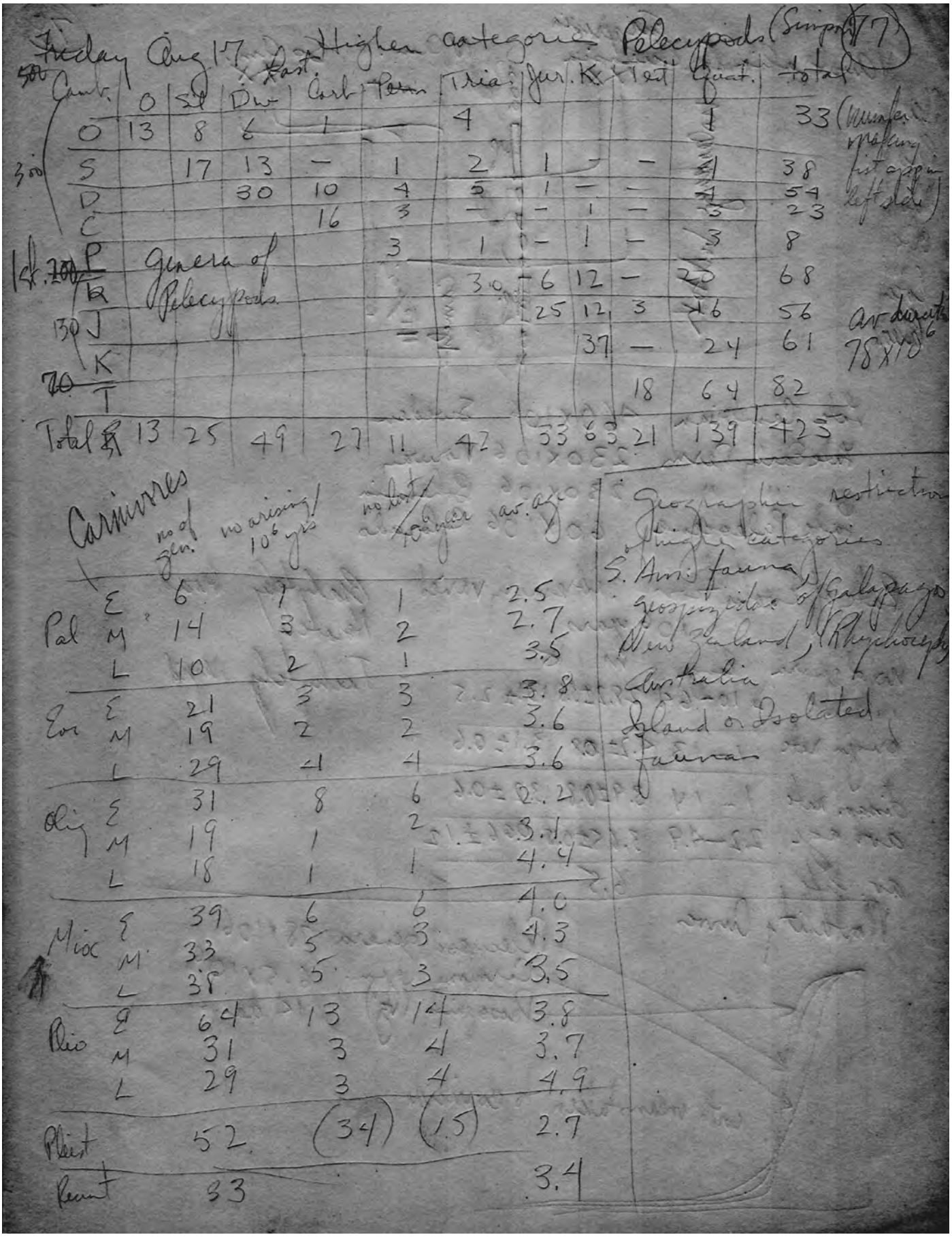
Serological reactions & closeness of homology

homology of chemistry Haemoglobin physiological

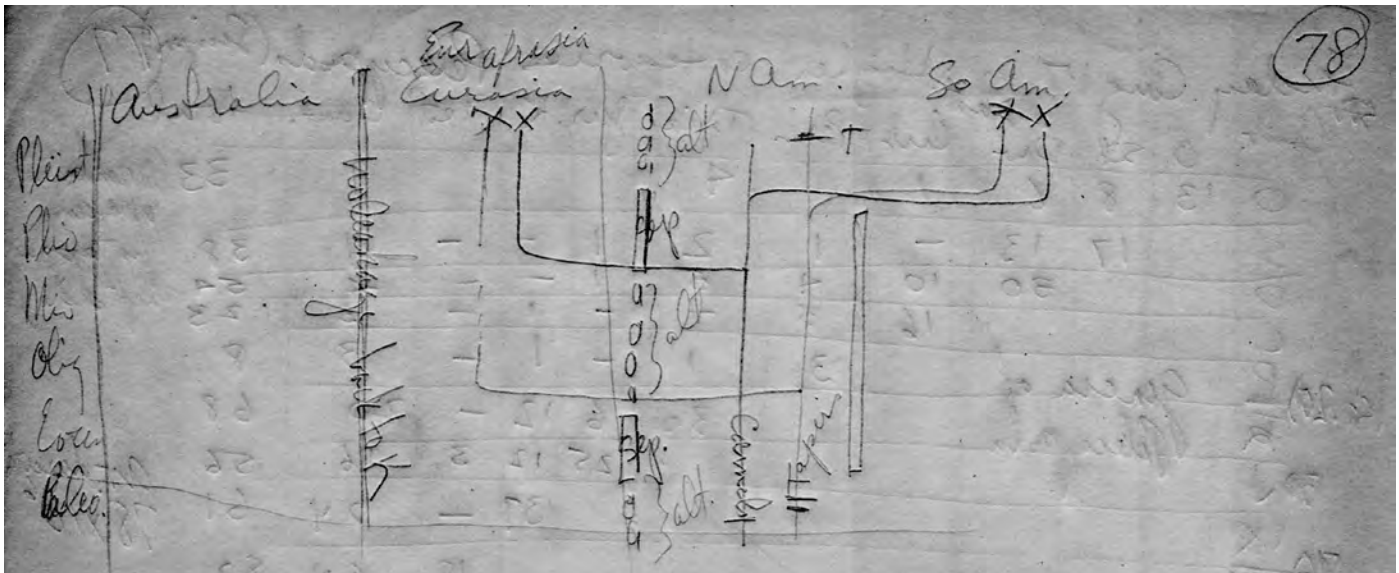
less satisfactory than morphological homologys.

due to the early origin of solutions to physiological problems.

Intracellular digestion of food particles


Friday Aug 17 Higher categories Pelecypods (Simpson 47)
Camb. O Sil Dev Carb Perm Tria Jur. Kr Tert Quat. total
O 13 8 6 1 4 1 33
S 17 13 — 1 2 1 — — 4 38
D 30 10 4 5 1 — — 4 54
C 16 3 — — 1 — 5 23
P 3 1 — 1 — 3 8
R 30 6 12 — 20 68
J 25 12 3 16 56
K 37 — 24 61
T 18 64 82
Total 13 25 49 27 11 42 33 63 21 139 423
Carnivores
no of gen. no arising/ 10⁶ yrs no ext/ 10⁶ yr av. age
Pal E 6 1 1 2.5
M 14 3 2 2.7
L 10 2 1 3.5
Eoc E 21 3 3 3.8
M 19 2 2 3.6
L 29 4 4 3.6
Olig E 31 8 6
M 19 1 2 3.1
L 18 1 1 4.4
Mioc E 39 6 6 4.0
M 33 5 3 4.3
L 38 5 3 3.5
Plio E 64 13 14 3.8
M 31 3 4 3.7
L 29 3 4 4.9
Pleist 52 (34) (15) 2.7
Recent 83 3.4
Geographic restriction
higher categories
S. Am. fauna
Galapagos
New Zealand, Rhynchocyp
Australia
Island or Isolated
faunas

78



Late Cambrian	460×10^6	Sweden
Late Early Perm	230×10^6	Norway
" "	230×10^6	Bohemia
Late Paleocene	60×10^6	Colorado

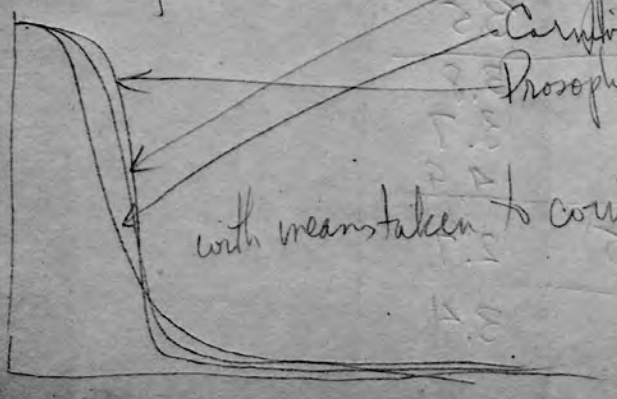
Rate of Evolution, extremely varied

Bradytely broad
Horotely
Tachytely rapid

10^6 years

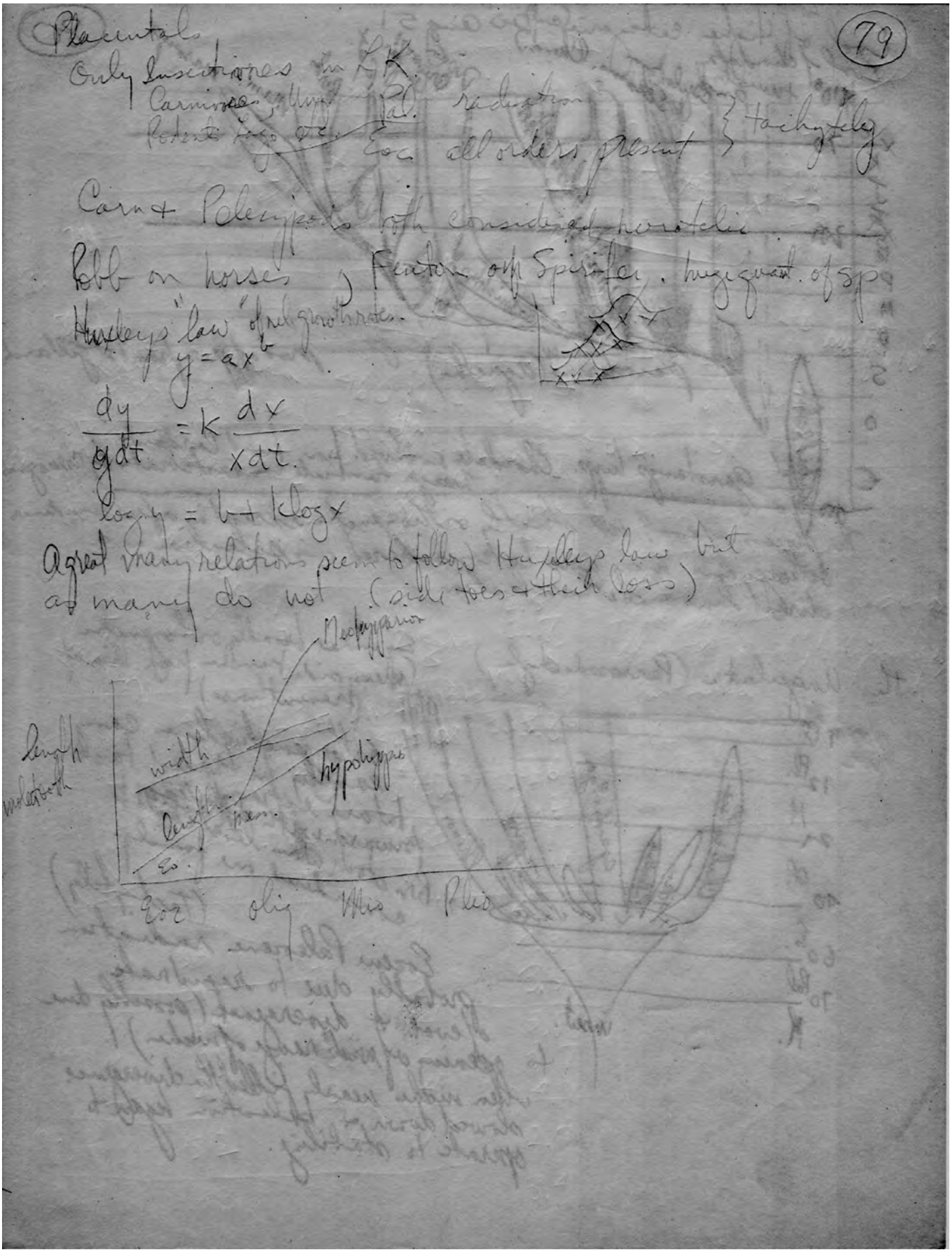
	range	m	σ
No of genera	> 10–64	28.2±3.5	131± 2.5
origin rate	1–13	4.2± 0.8	3.1± 0.6
dissap. rate	1–14	3.9±0.8	3.2 ±0.6
av age	2.2–4.9	3.65±0.18	.066 ±.12
av. life		6.5	

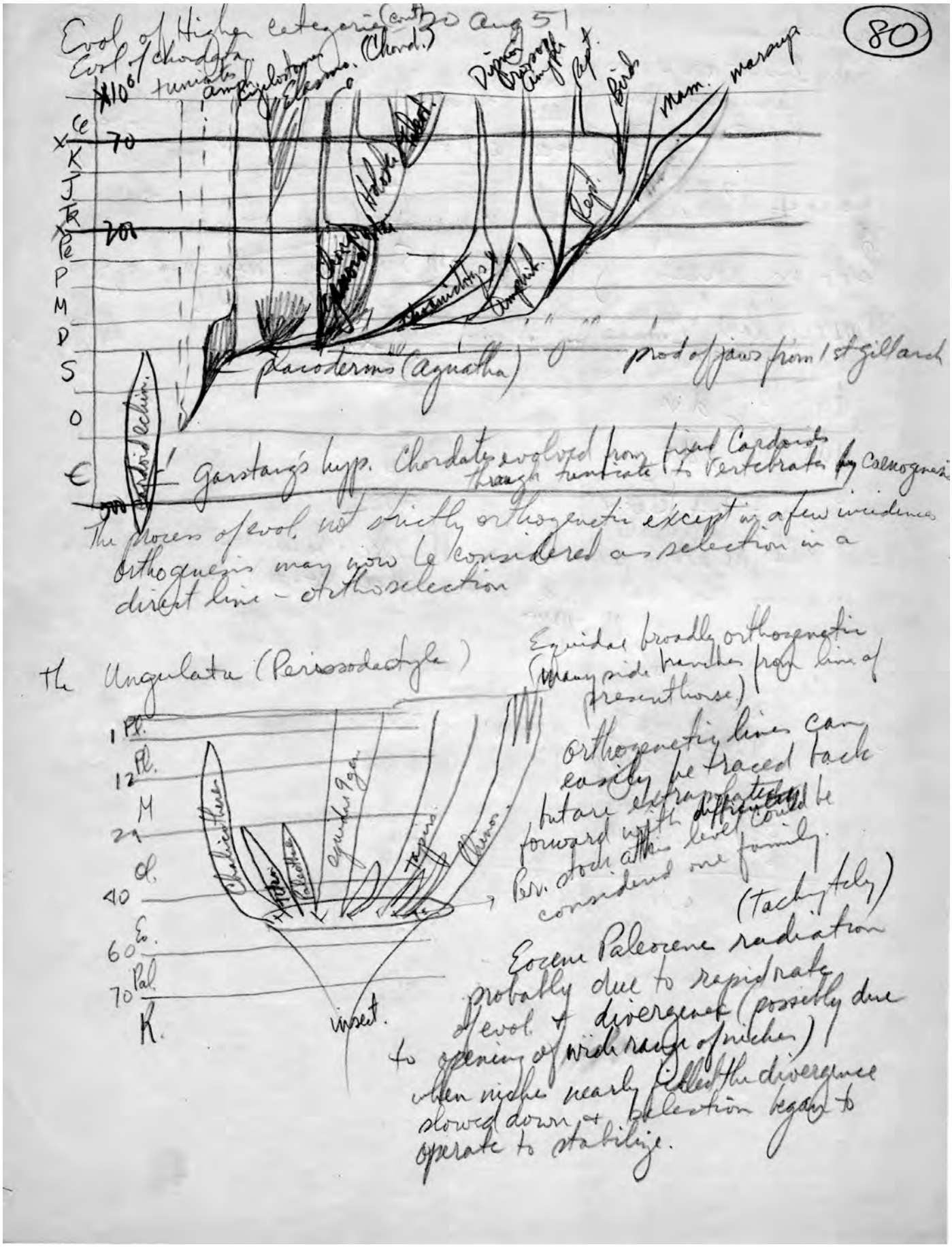
Mortality Curves



Pelecypod genera 78×10^6
Carnivore Gen. 6.5×10^6
Drosophila (Bz) 14 days

with means taken to coincide


Placentals
79
Only Insectivores in K.
Carnivora, Ungulata, Rodents Eoc. etc.
Eoc. radiation
all orders present
tachytely
Carn + Pelecypods both considered heterelic.
Rob on horses
Factor on Spirifer. magnitude of sp
Huxley's "law" of rel growth rates.
$y = ax^b$
$\frac{dy}{ydt} = k\frac{dx}{xdt}$
$\log y = b + k \log x$
A great many relations seem to follow Huxleys law but as many do not (side toes & their loss)
Neohipparion
length molar tooth
width
depth pen.
hypohippus
Eo.
Eoc
olig
Mio
Plio


Evol. of Higher categories (cont.) 30 aug 51
Evol. of chordata
(Chord.)
Diprotodon
Kangaroo
Rept.
Birds
Mam. marsup
Placoderms (Agnatha)
prod of jaws from 1st gill arch
Garstang's hypo. Chordata evolved from larval Cardiata through tunicate to vertebrate by Colnogenesis
The process of evol. not strictly orthogenetic except in a few instances
Orthogenesis may now be considered as selection in a direct line - orthoselection
The Ungulata (Perissodactyla)
Equidae broadly orthogenetic
(Many side branches from line of present horse)
orthogenetic lines can easily be traced back but are extrapolated forward with difficulty
Perr. stock at this level could be considered one family
(Tachyrhythy)
Eocene Paleocene radiation probably due to rapid rate of evol. + divergence (possibly due to opening of wide range of niches)
when niche nearly filled the divergence slowed down & selection began to operate to stabilize.
inset.

81

10% of diversification, 90% elaboration in neo-orthogenetic direction. (= orthoselection)

	Time to Divergence from com. anc.	life
Subspecies	10^3–10^4 years	10^4–10^5
Species	10^5	10^5–10^6
Genus	10^6	10^7–10^8
Family	10^7	10^8
Order	$10^{7.5}$	10^8
Class	10^8–10^9	10^8–9
Phylum	10^9	$> 10^9$ +

11000 fold Horotelic evol.

100 fold Tachytelic evolution

Higher categories probably arose by tachytely, periods of extremely rapid evolution / adaptive radiation.

a/alternative to mystical orthogenesis — 90% of cases — mystical emergence — 10% of cases.

by people impressed with descriptive terms

Horotely, periods of gradual change

Tachytely

elimination of usual higher categories.

emergence → adaptive radiation → orthogenesis

ecologic opportunity.

repitition of cycle.

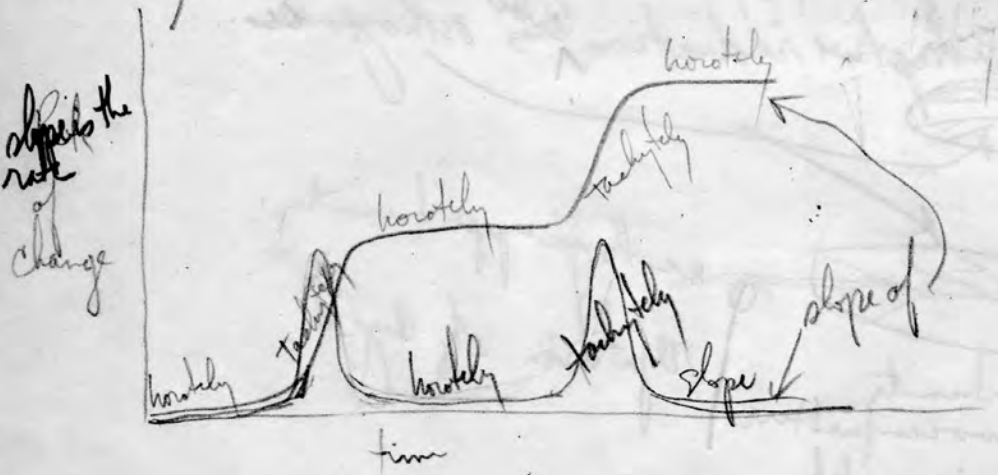
ecological opportunity
1. new way of life
2. attainment of unoccupied terr.
3. Preadapt to new envirs. coexist.

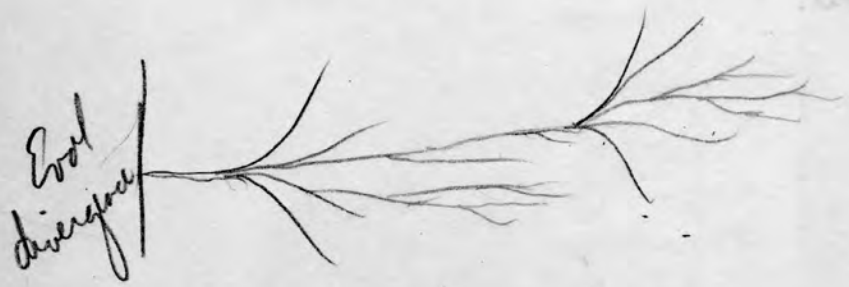
(82)

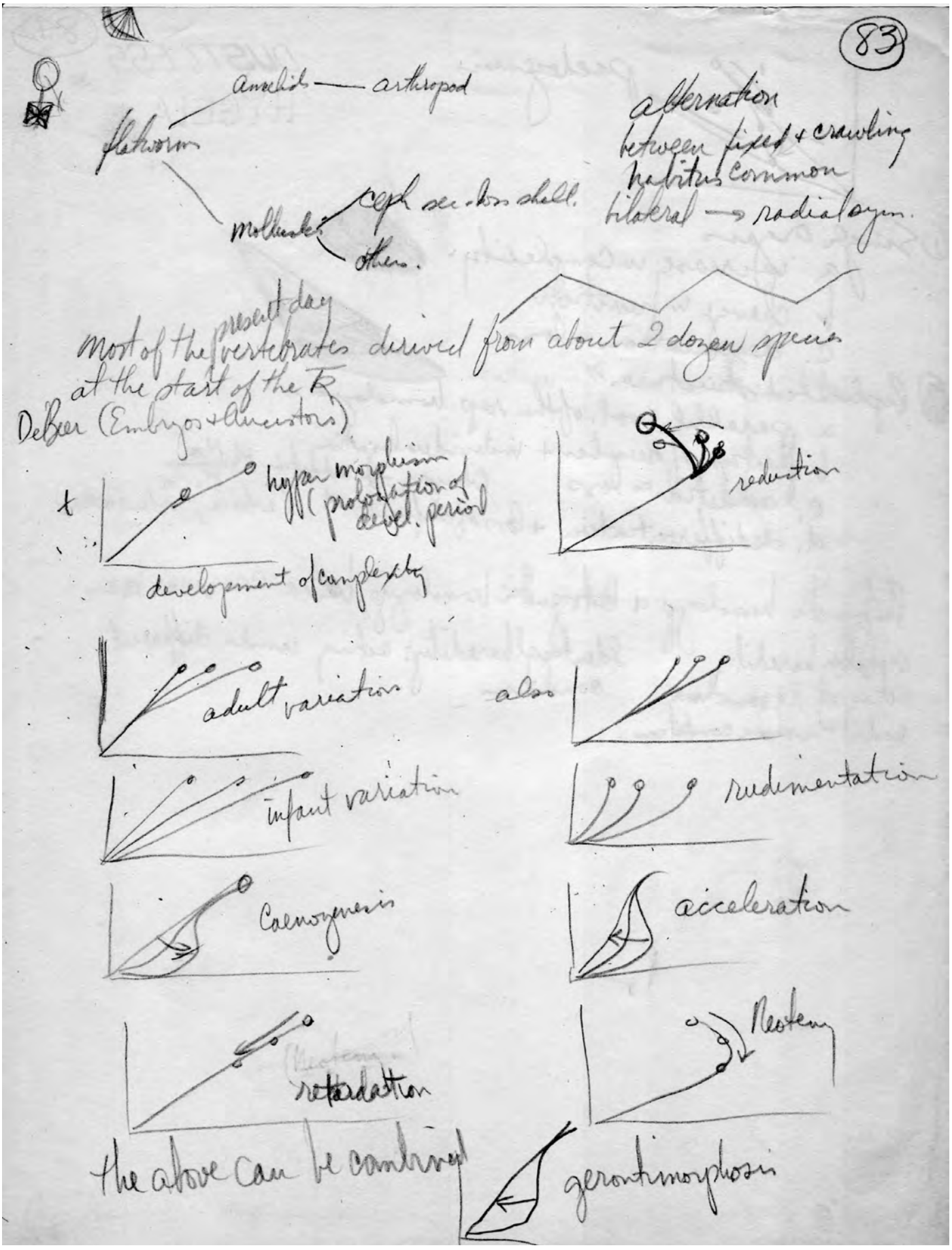
Classes	Super orders			orders			families		
	p.	ex.	tot.						
Agnatha	1	1	2	1	4	5	2	15	17
Placoderms	0	1	1	0	6	6	0	30	30
Chondrichthyes	2	0	2	3	3	6	30	16	46
Osteichthyes	4	0	4	12	5	17	368	80	448
Amphibia	2	1	3	3	10	13	20	48	68
Reptiles	3	3	6	4	12	16	49	145	154
Aves	2	2	4	27	7	34	162	35	197
Mammalia	3	3	6	17	14	31	110	122	232
	17	11	28	67	61	128	741	491	1232

16 of these 67 living orders provide over 75% of the living Chordates.

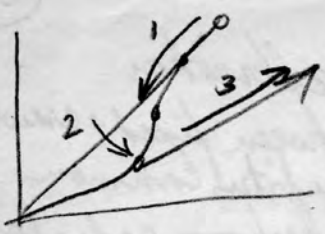
tachytely
emergence - adaptive radiation - selective elimination (appropriate categories)
orthogenesis - bradytely
horotely






(83)
annelid — arthropod
flatworm
mollusk
cephs
sec. loss shell.
others.
alternation
between fixed + crawling
habitus common
bilateral → radial asym.
Most of the present day vertebrates derived from about 2 dozen species at the start of the K
DeBeer (Embryos + Ancestors)
t
hyper morphism (prolongation of devel. period
development of complexity
reduction
adult variation
also
infant variation
rudimentation
Caenogenesis
acceleration
retardation
Neoteny
the above can be combined
gerontomorphosis

(84)



paedogenesis

DUSTLESS
HYGEIA

1) Single organs
   a increase in complexity
   b change in function
   c. degeneration + loss

2) Replicated structures
   a parallel evol. of the rep. homologues.
   b. fixation of number + individualization
   c. addition + loss. Otonyan ⇄ addition of $\frac{M_4}{M_4M_5}$
   d. dedifferentiation + loss of definite # (whales, edentates)

Phylogenetic homologys & Ontogenetic homologys have a common basis
similar heredity
acting at the same time
under the same conditions.

Identical heredity's acting under different conditions

Monday 27 Aug 51 Exam 2 to 4 Friday 31 Aug. (85)
Term papers due then.

Genus (sympatric as well as allopatric species)
Species group (Arctenkreis) (allopatric species)
Species (Lassenkreis) (Typically polytypic / occasionally monotypic. / Typically allopatric sp. not infrequently including sympatric subspecies (ring spec.)
Subspecies (step boundary (narrow transition zone) clines
Local race (elements in an orderly cline / random differentiation)
Neighborhood, deme (Neighborhood applied in a continuum to the region from which the parents could have come, deme in a population separated into more or less discrete units.

variety a term that's essentially obsolete, has been used for subspecies and also for segregating variant such as albinism
all the genetic mechanisms observed in lab appear in these categories.
accumulation of translocation leads to semi sterility since pairing rendered difficult. Gene mutations seem to be the ultimate basis of evolution. ~~the other~~ Multiple factor differences the most important.

Composition of Panmictic Mendelian populations
Hardy Weinberg law $(pa + qA)^2$
single loci mult allele, sex linkage
2 factors, mult. loci, r,
even with close linkage (17.) random recomb occurs
well within geol. time (69 gen.)
Composition of non panmictic
AA $(1-F)q^2 + Fq$ F is inbreeding coeff.
Aa $2(1-F)$
aa $(1-F)p^2 + Fp$

(86)

Δq = change in gene freq. per generation is yardstick for the processes of evolution.

(A) Systematic pressures

Δq determ.

recurrent Mutation pressure linear

Intrapopulation selection non-linear

Interpopulation (immigration) linear & crossbreeding

① $\Delta q = v(1-q) - uq - m(q - q_i) + \frac{q(w - \bar{w})}{\bar{w}} = 0$ for q

(B) Fluctuations

δq indet in dir. $\sigma_{\delta q}^2$ determ (in principle) negligible in bge panmictic pop.

② $\sigma_{\delta q}^2 = \frac{q(1-q)}{2N}$

$\hat{q} = \frac{v}{u+v}$

$\hat{q} = q_i$

$\hat{q} = \frac{v}{s}$ (dom.) $\sqrt{\frac{v}{s}}$ semi dom.

$\hat{q} = \frac{\frac{1}{s}}{\sum \frac{1}{s}}$

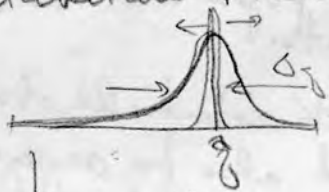
$\Delta q = s_q(1-q)$; $\sigma_{\Delta q}^2 = \sigma_s^2 q^2 (1-q^2)$

(C) "Unique events" wholly indet.

too infrequent to be included in above.

Amphidiploidy mass extinction + reestablishment

(D) Resultant of (A) + (B)



③ $\varphi(q) = \frac{C}{\sigma_{\delta q}^2} e^{2\int \frac{\Delta q}{\sigma_{\delta q}^2} dq}$ for a single pair of alleles

④ $\varphi(q) = C\, \bar{w}^{2N}\, q^{4N(m q_i + v) - 1} (1-q)^{4N[m(1-q_i) + u] - 1}$

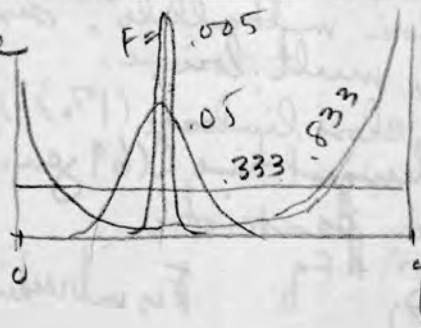
subs. ① + ② in ③

for all loci, mult. alleles.

$\varphi(q) = C\, \bar{w}^{2N} \pi \left[q^{4Nm q_i - 1} \right]$

Population structure

Island model.

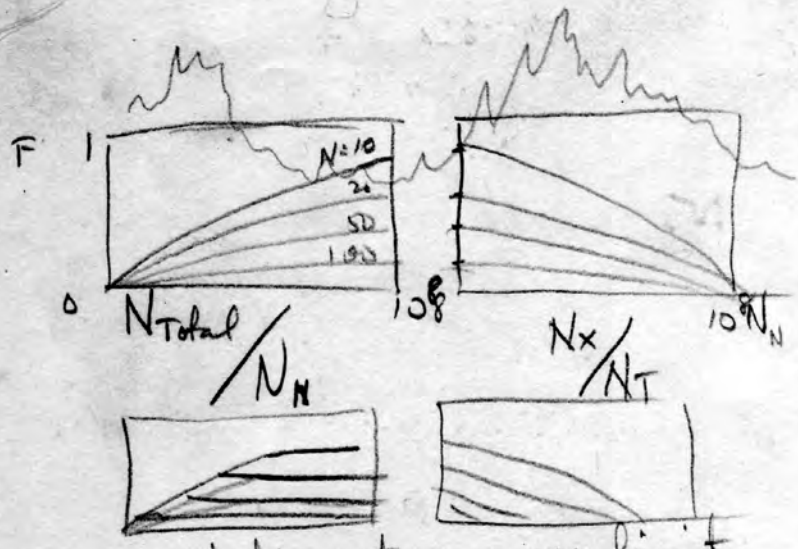


$F = \frac{1}{4Nm+1}$

Isolation by distance

87

little beyond Neighborhood of 200 very much at N = 20



mutation sets an upper limit.

more opportunity for differentiation in populations of linear extent

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Wed 29 Aug. 51 Evolution of the Mind

T. Edinger + Evol of Horse Brain

Association of the highest brains + minds outside of man (& man)

the evol. of the hand in Primates.

brachiating, erect posture, mind (intelligence)

input

invention of symbolism → Evolution of Ideas ("Essential diff. betw. M + An.")

tradition associated here:

any process of cumulative change can be called Evolutionary.

balance between isolation + interchange of ideas

something over 50% of intelligence derived from parents, equally set environment. (Wirtz)

Isolation by distance

assumptions ① Uniform density over a domain infinite with respect to dispersion

② Eggs or sperm released for dispersion, disperse while to form a fixed organism

2b Animal travels about the domain such that the distance from the position at birth and the position at time of mating has a normal distribution

Case 1 — Isotropic domain, no difference in properties with direction

T. Parents are to be found with a probability of .01 within a circle of radius 2σ (area $= 4\pi\sigma^2$)

F-2 parents (grandparents) are to be found with the same prob within a circle of radius $2\sqrt{2}\sigma$ $A = 8\pi\sigma^2$

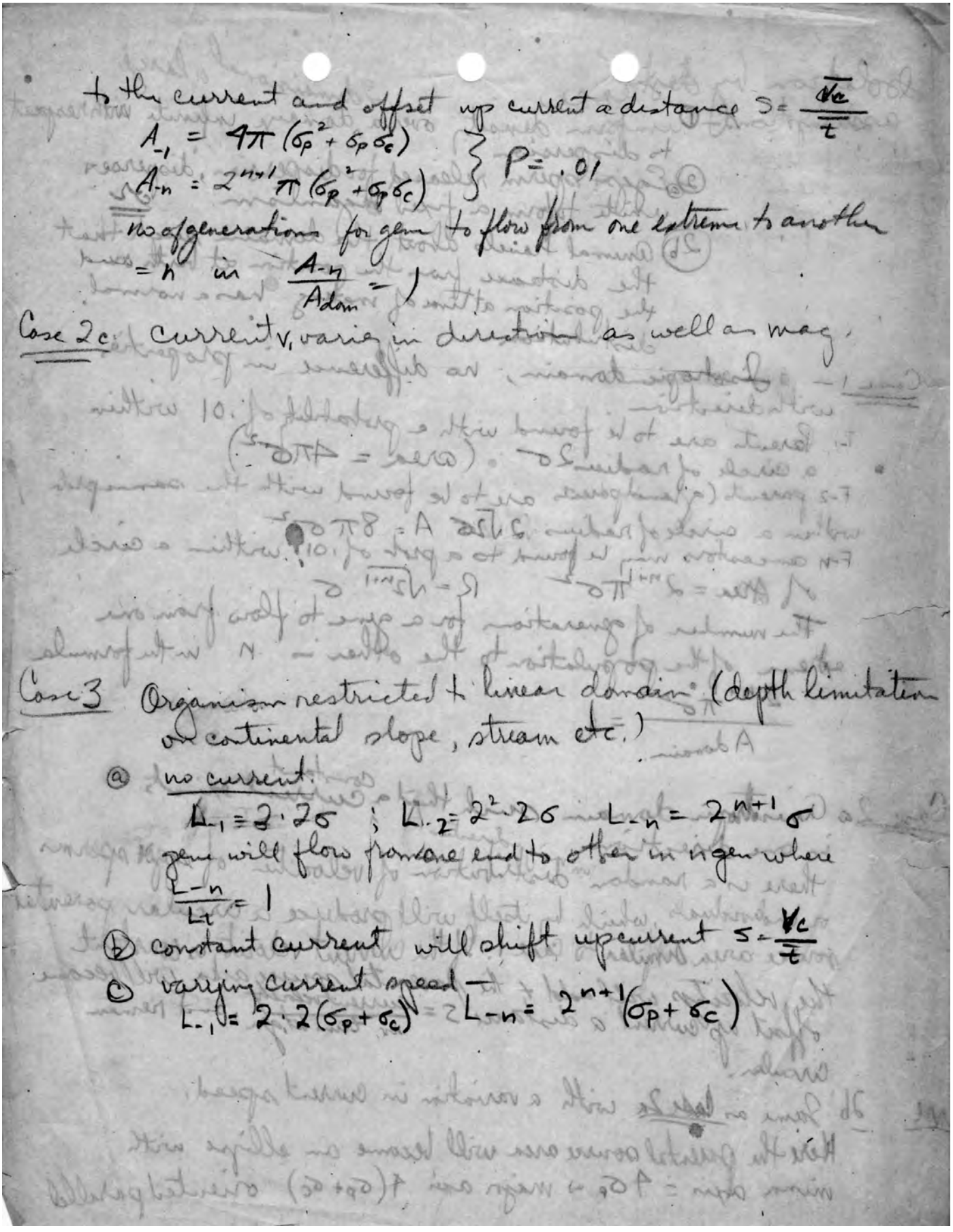
F-n ancestors may be found to a prob of .01 within a circle of Area $= 2^{n+1}\pi\sigma^2$ $R = \sqrt{2^{n+1}}\,\sigma$

The number of generations for a gene to flow from one extreme of the population to the other = n in the formula

$$\frac{2^{n+1}\cdot\pi\sigma^2}{A\ \text{domain}} = 1$$

Case 2a Anisotropic domain such that a constant current exists in one direction, there is a random distribution of velocities of eggs or sperm or individuals, which by itself will produce a circular parental source area similar to case 1. If the current velocity is constant the velocities will add & the parental source area will become offset up current a distance $S = \text{current velocity} \times \text{av. time to gen}$, and remain circular.

Case 2b Same as Case 2a with a variation in current speed. Here the parental source area will become an ellipse with minor axis $= 4\sigma_p$ & major axis $4(\sigma_p + \sigma_c)$ oriented parallel



+ the current and offset up current a distance $S = \frac{V_c}{t}$

$A_{-1} = 4\pi(\sigma_p^2 + \sigma_p\sigma_c)$

$A_{-n} = 2^{n+1}\pi(\sigma_p^2 + \sigma_p\sigma_c)$ } $P = .01$

no of generations for gen to flow from one extreme to another

$= n$ in $\frac{A_{-n}}{A_{dom}} = 1$

Case 2c: Current V_1 varies in direction as well as mag.

Case 3 Organism restricted + linear domain (depth limitation on continental slope, stream etc.)

(a) no current.

$L_{-1} = 2 \cdot 2\sigma$; $L_{-2} = 2^2 \cdot 2\sigma$ $L_{-n} = 2^{n+1}\sigma$

gen will flow from one end to other in n gen where

$\frac{L_{-n}}{L_t} = 1$

(b) constant current will shift upcurrent $S = \frac{V_c}{t}$

(c) varying current spread —

$L_{-1} = 2 \cdot 2(\sigma_p + \sigma_c)$ $L_{-n} = 2^{n+1}(\sigma_p + \sigma_c)$

APPENDIX

Final Examination. Zoology 313. Summer 1951.

1. Give the ultimate genotypic composition of large random breeding populations derived from the following initial compositions and not subject to any disturbing factors.

a. Equal frequencies of the sexes

			Unequal initial frequencies of the sexes				
			♀	♂	♀	♂
AA 60	AA 30	Aa^s 60	AA 160	20	AA 180	AY 30
aa 40	Aa 20	Aa 20	aa 40	80	aa 20	aY 70
	aa 50	a^sa 20				

b. How is equilibrium approached in these cases?

2. A population is made up with the following initial composition.

	♀	♂
AA BB	100	100
aa bb	100	100

a. What are the frequencies of genotypes at equilibrium and how is equilibrium approached if A and B are in different chromosomes?

b. What difference does it make in these respects if A and B are linked with 1% crossing over in both oogenesis and spermatogenesis?

3. Show by diagrams how gene frequency changes and give the value at equilibrium in the following cases in all of which gene A mutates to a at the rate 4×10^{-6} per generation.

a. Reverse mutation occurs at the rate 10^{-6} per generation.

b. AA has a 1% selective advantage over Aa and a 2% selective advantage over aa.

c. AA and Aa are alike and have a selective advantage of 1% over aa.

4. a. What is the variance of gene frequencies due to accidents of sampling in terms of gene frequency, q, and effective population number N, in a diploid random breeding population?

b. In a certain local population of moths the number of individuals that emerge as adults varies enormously from year to year. If the following estimates have been made over a period of 18 years, what is the indicated effective population number?

1000 in 10 of the years
100 in 5 of the years
10 in 3 of the years

5. a. Make a diagram to show the general nature of the probability distribution of a gene frequency in the long run in a population with a rather small effective population number (N), immigration at a low rate (m) from surrounding populations with gene frequency q_i = .10($4Nmq_i$ somewhat less than 1) and negligible selective differential.

b. Deal similarly with another gene of the same population for which the surrounding gene frequency is also .10 but which has a considerable selective advantage over its allele (4Ns much greater than 1).

6. a. List ways in which two or more alleles may be maintained in stable equilibrium in a large completely isolated random breeding population.

b. List ways in which different alleles may become nearly fixed in different partially isolated subdivisions of a species.

7. Compare briefly the possibilities for evolutionary transformation as a single species in the case of the two types of population described in 6a and 6b.

a. In the absence of secular change in the environment

b. In the presence of secular change in the environment

8. a. What (briefly) are meant today by the terms species and subspecies?

b. List several ~~correlations~~ conditions that give rise to difficulties in definition.

9. What is the genetic interpretation of homology

a. among different parts of the same organism?

b. among corresponding parts of different organisms?

c. Relate these interpretations briefly to major aspects in the evolution of teeth in the vertebrates.

10. Discuss briefly the problem of the origin of the higher categories. Illustrate by concrete cases.

R. E. Sloan
Assignment #1

1)

	♀	♂
AA	70	70
Aa	0	0
aa	30	30
	100	100

$[.70A + .30a]^2 = [.49AA + .42Aa + .09aa]$ ✓

	♀	♂	
AA	80	10	or 50%
Aa	0	0	
aa	20	10	or 50%
	100	20	100%

$[.8A + .2a][.5A + .5a] = [.40AA + .50Aa + .10aa]$ F_1 ✓

$\bar{q}_A = \frac{[.8 + .5]}{2} = .65$

	♀	♂	
AA	20 × 10	40	
Aa	40	20	40
aa	140	70	20
	200	100	100

$[.65A + .35a]^2 = [.42AA + .46Aa + .12aa]$ ✓

$\bar{q}_A = \frac{[.20 + .60]}{2} = .40$ ✓

$[.40A + .60a]^2 = [.16AA + .48Aa + .36aa]$

2)

A_	9900
aa	100
	10000

$(1-q)^2 = .01$
$1 - q = .1$
$q = .9$

$AA = (.9)^2 = .81$
$aa = .01$
$1 - .82 = .18 = Aa$ ✓

A_	9999
aa	1
	10000

$(1-q)^2 = aa = .0001$
$(1-q) = .01$
$q = .99$

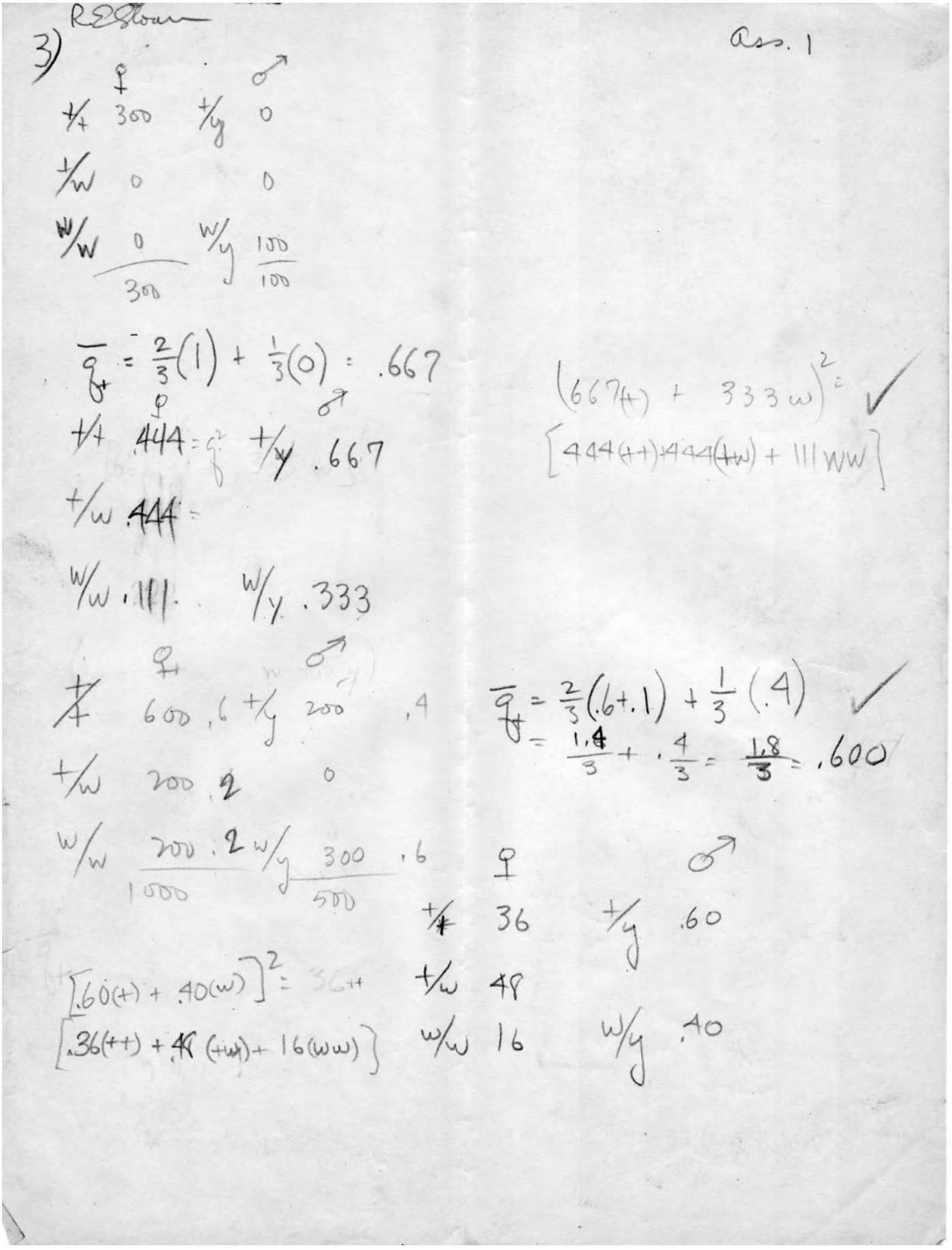
$AA = (.99)^2 = .9801$
$aa = .0001$
$.9802$
$Aa = .0198$ ✓

A_	256	
aa	144	.27
	400	1

$(1-q)^2 = aa = .27$ .36
$(1-q) = .52$ .60
$q = .48$ .40

$AA = (.48)^2 = .23$ .16
$aa = .27$ .36
.50 .52
$Aa = .50$ .48

$\frac{144}{400} = .36$


R.E. Glover
3)
Ass. 1
♀ ♂
+/+ 300 +/y 0
+/w 0 0
w/w 0 w/y 100
300 100
$\bar{q}_+ = \frac{2}{3}(1) + \frac{1}{3}(0) = .667$
♀ ♂
+/+ .444 = q^2 +/y .667
+/w .444 =
w/w .111 w/y .333
♀ ♂
+/+ 600 .6 +/y 200 .4
+/w 200 .2 0
w/w 200 .2 w/y 300 .6
1000 500
$[.60(+) + .40(w)]^2 = 36++$
$[.36(++) + .48(+w) + 16(ww)]$
$(667+) + 333w)^2 =$
$[444(++) + 444(+w) + 111ww]$
$\bar{q}_+ = \frac{2}{3}(.6+.1) + \frac{1}{3}(.4)$
$= \frac{1.8}{3} + \frac{.4}{3} = \frac{1.8}{3} = .600$
♀ ♂
+/+ 36 +/y .60
+/w 48
w/w 16 w/y .40

4) ♀ ♂

800	CCAa	.8	200	CcAA	.4
200	CCaa	.2	300	ccAA	.6
1000		1	500		1

$\bar{q}_C = \frac{[1 + .2]}{2} = .60$ $\quad [.6C + .4c]^2 = [.36CC + .48Cc + .16cc]$

$\bar{q}_A = \frac{[1 + .4]}{2} = .70$ $\quad [.7A + .3a]^2 = [.49AA + .42Aa + .09aa]$

		AA (.49)	Aa (.42)	aa (.09)
.36	CC	.177	.151	.032
.48	Cc	.236	.201	.043
.16	cc	.078	.067	.014

5)

900	C_A_ agouti	.9	$q_c^2 = .04$ $\quad q_c = .2$ + $p_C = .8$
60	C_aa black	.06	
40	cc → white	.04	$q_a^2 = .0625$ $\quad q_a = .25$ + $p_A = .75$
1000		1	(60 out of 960)

$(.8C + .2c)^2 = (.64CC + .32Cc + .04cc)$

$(.75A + .25a)^2 = (.563AA + .374Aa + .063aa)$

		.64 CC	.32 Cc	.04 cc
.563	AA	.360	.180	.023
.374	Aa	.240	.120	.015
.063	aa	.040	.020	.002

black

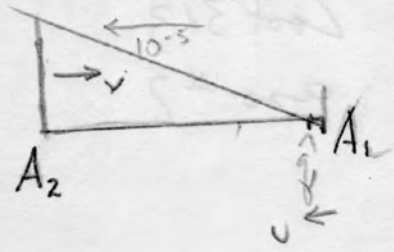
agouti

.02374 626
A 374
.015
.06
.0021

.036

R. E. Glover
Ans. #2

(1) $A_1 \xrightarrow{10^{-6}} A_2$



$\Delta q = 10^{-5}(1-\hat{q}_1) - 10^{-6}\hat{q}_1 = 0$

$10^{-5} - 10^{-5}\hat{q}_1 = 10^{-6}\hat{q}_1$

$10^{-5} = \hat{q}_1(10^{-5} + 10^{-6})$

$\hat{q}_1 = \frac{10^{-5}}{10^{-5}+10^{-6}} = \frac{.000010}{.000011} = .909$ ✓

(2) $A_1 \longrightarrow A_2$ 10^{-5}/generation

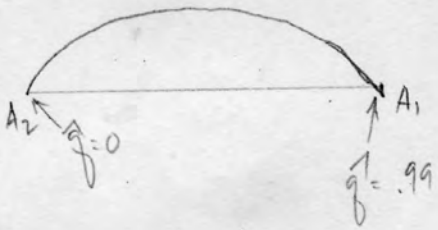
	w	
A_1A_1	1.002	$1+2s$
A_1A_2	1.001	$1+s$
A_2A_2	1.000	

$\Delta q_1 = -10^{-5}q_1 + (.001)q_1(1-q_1) = q_1(-10^{-5} + (.001)(1-q_1))$

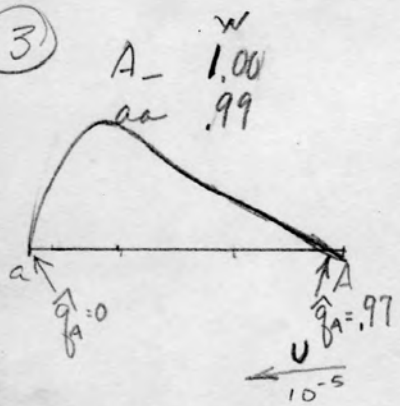
at equil. $\Delta q_1 = 0$ & $\hat{q} = 0$ or

$10^{-5} = 10^{-3}(1-q_1)$ ✓

$1 - q_1 = 10^{-2}$; $\hat{q}_1 = .99$



(3)



	w
$A_$	1.00
aa	.99

$\bar{w} = 1 - .99q_a^2$

$w_a = .99q_a$

$\Delta q_a = u(1-q_a) - .01q_a \cdot q_a(1-q_a)$

$10^{-5}(1-q_a) = .01q_a^2(1-q_a)$ ✓

$\hat{q}_a = 1$ & $\hat{q}_a^2 = \frac{10^{-5}}{10^{-2}} = 10^{-3} \cong .03$

R E Sloan
Ass #2

(3)

		W	
A_1A_1	q_1^2	60	1-40
A_1A_2	$2q_1q_2$	100	1
A_2A_2	q_2^2	80	1-20

$\bar{W} = 1 - .40q_1^2 - .20(1-q_1)^2 =$

$\Delta q_1 = \dfrac{q_1(.60 - (1 - .40q_1^2 - .20(1-q_1)^2))}{1 - .40q_1^2 - .20(1-q_1)^2}$

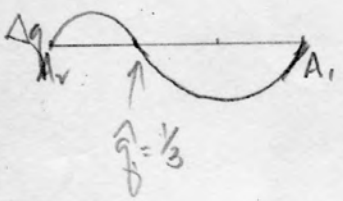
$\bar{W} = 1 - .40q_1^2 - .20 + .40q_1 - .20q_1^2$

$= -.60q_1^2 + .40q_1 + .80$

$= \dfrac{q_1[.60 - .80 - .40q_1 + .60q_1^2]}{-.60q_1^2 + .40q_1 + .80}$

$= \dfrac{q_1[.60q_1^2 - .40q_1 + .20]}{\bar{W}}$

$= \dfrac{q_1(1-q_1)(-.60q_1 + .20) = 0}{\bar{W}}$



$\hat{q}_1 = 0\ ;\ 1\ ;$ or $\hat{q}_1 = 1/3$

RE Sloan ①

Ass #3

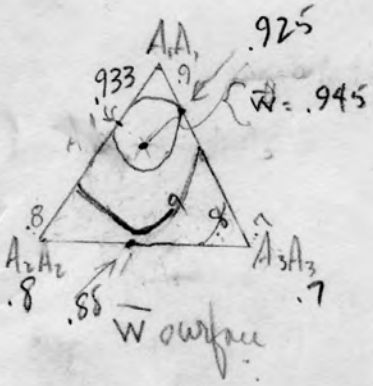
①

A_1A_1	.90	$1-s_1$	$s_1=.1$
A_1A_2	1.00		
A_1A_3	1.00		
A_2A_2	.80	$1-s_2$	$s_2=.2$
A_2A_3	1.00		
A_3A_3	.70	$1-s_3$	$s_3=.3$

$$\hat{q}_1 = \frac{1/s_1}{\sum 1/s} = \frac{10}{10+5+10/3} = \frac{10}{18.33} = .545$$

$$\hat{q}_2 = \frac{5}{18.33} = .272$$

$$\hat{q}_3 = \frac{3.33}{18.33} = \frac{.182}{.999}$$



$w_1 = w_2 = w_3 = \bar{w}$ at equil.

$$w_1 = \bar{w} = 1 - s_1 q_1$$
$$= 1 - .0545 = .9455$$

when 3 is lost

$$\hat{q}_1 = \frac{1/s_1}{\frac{1}{s_1}+\frac{1}{s_2}} = \frac{10}{10+5} = 2/3 = .666$$

$$w_1 = 1 - .0666 = .9333$$

when 2 is lost.

$$\hat{q}_1 = \frac{1/s_1}{\frac{1}{s_1}+\frac{1}{s_3}} = \frac{10}{10+3.3} = .75$$

$$w_1 = 1 - .075 = .925$$

when 1 is lost

$$\hat{q}_2 = \frac{1/s_2}{\frac{1}{s_2}+\frac{1}{s_3}} = \frac{5}{8.3} = .60$$

$$w_2 = 1 - .12 = .88$$

Loan page (2)

2

		w_i
A_1A_1	q_1^2	1.10
A_1A_2	$2q_1q_2$	1.20
A_1A_3	$2q_1q_3$	1.25
A_2A_2	q_2^2	1.10
A_2A_3	$2q_2q_3$	1.10
A_3A_3	q_3^2	1.00

$$w_1 = \frac{w_{11}q_1^2 + w_{12}q_1q_2 + w_{13}q_1q_3}{q_1}$$

$= 1.10q_1 + 1.20q_2 + 1.25q_3$

$= 1.10q_1 + 1.20q_2 + 1.25(1 - q_1 - q_2)$

$= 1.10q_1 + 1.20q_2 + 1.25 - 1.25q_1 - 1.25q_2$

(1) $= 1.25 - .15q_1 - .05q_2$

$w_2 = 1.10q_2 + 1.20q_1 + 1.10(1 - q_1 - q_2)$

$= 1.10q_2 + 1.20q_1 + 1.10 - 1.10q_1 - 1.10q_2$

(2) $= .10q_1 + 1.10$

$w_3 = 1.25q_1 + 1.10q_2 + 1(1q_1 - q_2)$

(3) $= .25q_1 + .10q_2 + 1$

(2) − (1) $= .25\hat{q}_1 + .05\hat{q}_2 = .15$

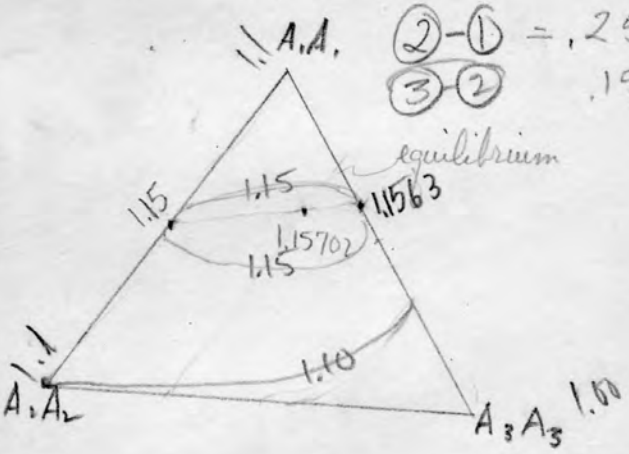
(3) − (2) $.15\hat{q}_1 + .10\hat{q}_2 = .10$

$\hat{q}_1 = \frac{3 - \hat{q}_2}{5}$

$\hat{q}_2 = 1/7$ ✓

$\hat{q}_1 = 4/7$ ✓

$\hat{q}_3 = 2/7$ ✓



$$\bar{W} = 1 + s_{11}q_1^2 + 2s_{12}q_1q_2 + 2s_{13}q_1q_3 + s_{22}q_2^2 + 2s_{23}q_2q_3 + s_{33}q_3^2$$

at equil $\bar{W} = 1 + .10\frac{16}{49} + .40\frac{4}{49} + .50\frac{8}{49} + .10\frac{1}{49} + .20\frac{2}{49} + 0$

$= 1 + .03261 + .03261 + .0816 + .00204 + .00816 = 1.15702$ ✓

when A_3 absent $\hat{q}_1 = .5$ $\hat{q}_2 = .5$

$\bar{W} = 1 + .10(.5)^2 + .40(.5)^2 + .10(.5)^2 = 1 + .025 + .1 + .025 = 1.15$ ✓

when A_2 absent $\bar{W} = -.4q^2 + .5q + 1$ $w_1 = -.15q + 1.25$

$\Delta q = q(q-1)(.4q - .25) = 0$ for $q = 0, 1, \text{ & } \hat{q} = 5/8$

$\bar{W}$ at $q = 5/8 = 1\frac{10}{64} = 1.1563$ ✓

Sloan ③

② cont

when A_1 absent $\bar{w} = 1.10q^2 + 2.20q(1-q) + (1-q)^2$

$= 1.10q^2 + q^2 - 2.20q^2 + 2.20q - 2q + 1$

$= -.10q^2 + .2q + 1$

$w_2 = \frac{1.10q^2 + 1.10q(1-q)}{q} = 1.10q + 1.10 - 1.10q = 1.10$

$\Delta q = \frac{q(1.10 + .1q^2 - 2q - 1)}{\bar{w}} = \frac{.1q(q^2 - 2q + 1)}{\bar{w}}$

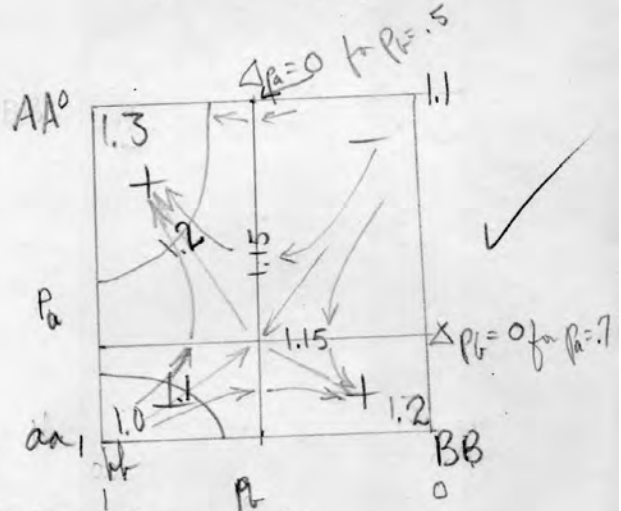
$= \frac{.1q(q-1)^2}{\bar{w}} = 0$ for $q = 0$ + $q = 1$

There is no equilibrium point between the values $q=0$ & 1 ✓

This is stable only when A_2 or A_3 is fixed and the adaptive values are all in favor of fixation of A_2

③

	w	f
A_ B_	1.1	$(1-p_a^2)(1-p_b^2)$
A_ bb	1.3	$(1-p_a^2)p_b^2$
aa B_	1.2	$p_a^2(1-p_b^2)$
aa bb	1.0	$p_a^2 p_b^2$



$\bar{w} = 1.1(1 - p_b^2 - p_a^2 + p_a^2 p_b^2) + 1.3(p_b^2 - p_a^2 p_b^2)$

$+ 1.2(p_a^2 - p_a^2 p_b^2) + p_a^2 p_b^2$

$= 1.1 + p_b^2(-1.1 + 1.3) + p_a^2(-1.1 + 1.2) + p_a^2 p_b^2(1.1 - 1.3 - 1.2 + 1)$

$= 1.1 + .2p_b^2 + .1p_a^2 - .4p_a^2 p_b^2$ ✓

$\frac{\partial \bar{w}}{2\partial p_a} = .1p_a - .4p_a p_b^2 = p_a(.1 - .4p_b^2) = 0$ for $p_a = 0$ + $p_b = \sqrt{\frac{1}{4}} = \frac{1}{2}$

$\Delta p_a = \frac{p_a(1-p_a)\left(\frac{\partial \bar{w}}{2\partial p_a}\right)}{2\bar{w}} = 0$ for $p_a = 0$, $p_a = 1$ + $\frac{\partial \bar{w}}{2\partial p_a} = 0$ ✓

$\frac{\partial \bar{w}}{2\partial p_b} = .2p_b - .4p_a^2 p_b = p_b(.2 - .4p_a^2) = 0$ for $p_b = 0$ + $p_a = \sqrt{\frac{2}{2}} = .707$

$\Delta p_b = \frac{p_b(1-p_b)\left(\frac{\partial \bar{w}}{2\partial p_b}\right)}{2\bar{w}} = 0$ for $p_b = 0, 1$ + $\frac{\partial \bar{w}}{2\partial p_b} = 0$

Sloan page (4)

(3) cont

$\bar{W} = 1.1 + .2\left(\frac{1}{4}\right) + .1\left(\frac{1}{2}\right) - .4\left(\frac{1}{4}\cdot\frac{1}{2}\right)$ at $p_a = .707$, $p_b = .5$

$= 1.1 + .05 + .05 - .05 = 1.15$

since $\frac{\partial \bar{w}}{2\partial p_a} = 0$ for $p_b = .5$ the values of $\bar{w}$ along the line $p_b = .5$ are constant & = to 1.15

similarly for $\frac{\partial \bar{w}}{2\partial p_b}$ + the line $p_a = .707$

(4)

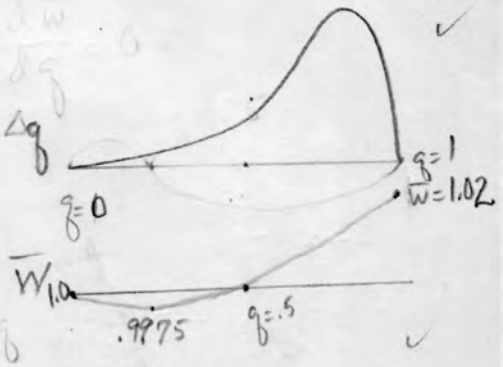
		w	
A_1A_1	q^2	$1 + .02q$	$s_{11} = .02q$
A_1A_2	$2q(1-q)$	1	$s_{12} = 0$
A_2A_2	$(1-q)^2$	$1 - .02q$	$s_{22} = -.02q$

$\bar{W} = (1+.02q)q^2 + 2q(1-q) + (1-.02q)(1-2q+q^2)$

$= q^2 + .02q^3 + 2q - 2q^2 + 1 - .02q - 2q + .04q^2 + q^2 - .02q^3$

$= .04q^2 - .02q + 1$

$\frac{d\bar{W}}{dq} = .08q - .02 = 0$ for $q = 1/4$



$\bar{w}$ for $q = .25 = 1 - .005 + .0025$

$w_1 = \frac{(1+.02q)q^2 + q(1-q)}{q}$

$= q + .02q^2 + 1 - q = .02q^2 + 1$

$\Delta q = \frac{q(.02q^2 + 1 - .04q^2 + .02q - 1)}{\bar{w}} = q(-.02q^2 + .02q)$

$\Delta q = 0$ for $q = 0$ & $q = 1$ & no others $= .02q^2(-q+1)$

Sloan page 5

⑤

A_1A_1	$1-.02q$	q^2
A_1A_2	1	$2q(1-q)$
A_2A_2	$1+.02q$	$(1-q)^2$ or $(1-2q+q^2)$

$\bar{w} = q^2 - .02q^3 + 2q - 2q^2 + 1 + .02q - 2q - .04q^2 + q^2 + .02q^3$

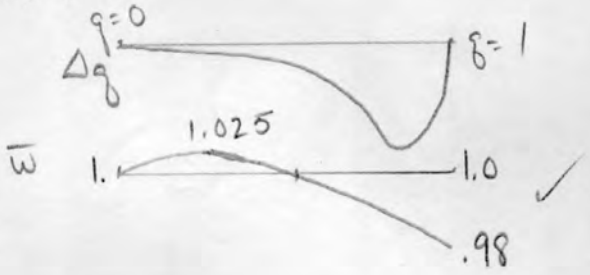
$= (1-2-.04+1)q^2 + (2+.02-2)q + 1 = -.04q^2 + .02q + 1$

$w_1 = \dfrac{(1-.02q)q^2 + q(1-q)}{q} = q - .02q^2 + 1 - q = -.02q^2 + 1$

$\Delta q = \dfrac{q(-.02q^2 + 1 + .04q^2 - .02q - 1)}{\bar{w}} = \dfrac{q(.02q^2 - .02q)}{\bar{w}}$

$= 0$ for $q = 0$, $q = 1$ another.

$\dfrac{d\bar{w}}{dq} = -.08q + .02 = 0$ for $q = .25$



⑥

A_1A_1	$1.01(1-.04q)$	q
A_1A_2	$1 \quad (1-.04q)$	$2q(1-q)$
A_2A_2	$.99(1-.04q)$	$(1-q)^2$ or $(1-2q+q^2)$

$\bar{w} = (1-.04q)[1.01q^2 + 2q - 2q^2 + .99 - 1.98q + .99q^2]$

$= (1-.04q)[.02q + .99] = -.0008q^2 - .0196q + .99$

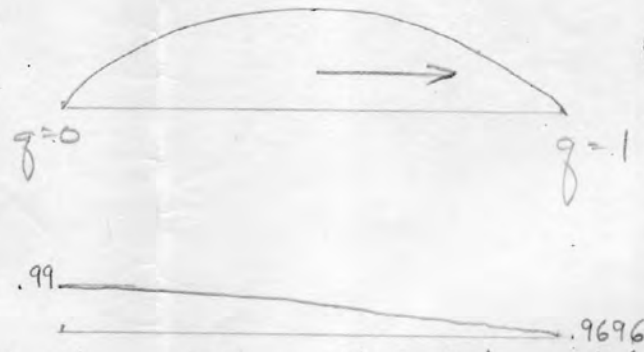
$w_1 = \dfrac{(1-.04q)[1.01q^2 + q(1-q)]}{q} = (1-.04q)(1.01q - q + 1) = (1-.04q)(1+.01q)$

$\Delta q = \dfrac{q(1-.04q)(1+.01q-.99-.02q)}{\bar{w}} = \dfrac{q(1-.04q)(.01-.01q)}{\bar{w}}$

$= 0$ for $q = 0$, $q = 1$ $q = 25$ (meaningless.)

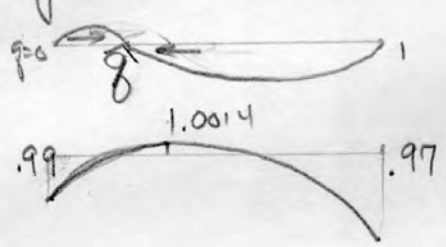
(6) cont. Slow on page (6)

$$\frac{d\bar{w}}{dq} = -.0016q - .0196 = 0 \text{ for } q = -\frac{196}{16} \text{ (meaningless outside limits of } q\text{)}$$



There is a trend to fixation of A_1 even though it is deleterious to the population as a whole.

(7)



A_1A_1	$1.01 - .04q$	q^2
A_1A_2	1	$2q(1-q)$
A_2A_2	$.99 + .04q$	$(1-q)^2 = (1 - 2q + q^2)$

$$\bar{w} = 1.01q^2 - .04q^3 + 2q - 2q^2 + .99 + .04q - 1.98q - .08q^2 + .99q^2 + .04q^3$$
$$= q^2(1.01 - 2 + .99 - .08) + q(2 + .04q - 1.98) + .99$$
$$= -.08q^2 + .06q + .99$$

$$w_1 = [(1.01 - .04q)q^2 + q(1-q)]/q = -.04q^2 + .01q + 1$$

$$\Delta q = \frac{q[(-.04 + .08)q^2 + (.01 - .06)q + (1 - .99)]}{\bar{w}} = \frac{q(.04q^2 - .05q + .01)}{\bar{w}}$$

$$= \frac{.01q(1-q)(1-4q)}{\bar{w}} = 0 \text{ for } q = 0, 1, \text{ or } 1/4$$

$$\frac{d\bar{w}}{dq} = -.16q + .06 = 0 \text{ for } q = \frac{6}{16} = 3/8$$

$$\bar{w} \text{ for } q = 3/8 = -.08\frac{9}{64} + .06\frac{3}{8} + .99 = 1.0014$$

Here there is a near correspondence between the equilibrium point and the maximum $\bar{w}$

Critical Review of "The Evolution of Zaphrentis delanouei in Lower Carboniferous Times", by R. G. Carruthers.

Critical Review of "The Evolution of Zaphrentis delanouei in Lower Carboniferous times," by R. G. Carruthers.

Carruthers' paper is a classic example of a well worked out temporal sequence of populations. He is working with a group of four "species" of Rugose corals from the Lower Carboniferous of the Central Valley of Scotland. Carruthers sets up four mutations (in the sense of Waagen, not De Vries) to each of which he assigns a binomial. These "mutations" vary in frequency in a regular way in space and time. Carruthers appears to consider each of these "mutations" a separate species, a conclusion that seems to be unwarranted by his data.

The group of species of Rugose corals that Carruthers discusses has a number of characters that remain constant; average size and shape, (conical at first and later cylindrical); an epitheca with clearly marked longitudinal ribbing, the cardinal fossula is on the concave side of the corallum, the spacing and character of the tabulae (arched upwards and depressed into the fossula), the septa thickened at the inner end and the septa curved convex to the cardinal fossula. The differences that Carruthers noted and made the basis of his species are the shape of the cardinal fossula and the length of the major septa.

The earliest member of this species group occurs in the Cementstone Group and is Z. delanouei; it has the septa meeting in the center of the corallum and a large cardinal fossula expanded at the inner end. Associated with Z. delanouei but less common in Z. parallela with the walls of the fossula parallel or faintly constricted at the inner end.

After a considerable gap in the stratigraphic sequence the group appears again in the Lower Limestone Group of the Carboniferous Limestone series. Z. delanouei and Z. parallela are still present but rare, Z. constricta is the predominant species. This species still has the septa joined together but the fossula is very much constricted at the inner end. Also present in the Lower Limestone Group is the fourth species Z. disjuncta, which has the constricta type of fossula but in which the septa retreat towards the walls of the corrallum. All of the characters listed above were determined at approximately the same diameter on the carallum, below the floor and in the conical portion. In the Upper Limestone Group of the Carboniferous Limestone Series Z. delanouei is absent, Z. parallela is extremely rare and Z. constricta is definitely subordinate to Z. disjuncta, the dominant form. At the last appearance of the species group in the Millstone Grit, Z. disjuncta is by far the most abundant species.

The vertical distribution of Carruthers' species is summarized in table I and figure 1. In the Lower Limestone Group especially there is a variation in the proportions of the species from East to West. This is indicated in table I by arranging the localities from East at th top to West at the bottom within each stratigraphis zone, and is further shown by figure 2.

On the basis of this information Carruthers concluded that there was an evolution from Z. delanouei to Z. disjuncta in the Lower Carboniferous of Scotland. This is warranted by his data. The method chosen by Carruthers is a convenient one for curatorial work but since his species are artificial

segments of naturally interbreeding populations, they do not correspond closely to present day species. A more advisable procedure might be to set up paleontological species as horizontal (i.e. temporally coexistent) grpups of local populations that intergrade imperceptible, with divisions between species occurring at major unconformities or when the species has changed sufficiently to warrant a new name. One method which has been suggested for the second alternative is to assign a new name when the mean value of a distinguishing character of a population differs significantly from the mean value of the same character of the type population when measured by an analysis of variance. This solution is still not quite satisfactory since the problem still remains of adapting a discontinuous system of nomenclature to a continuously varying set of populations. The situation here is a perfect example for the situations described by G. G. Simpson (1937) in a very useful paper.

Carruthers also concludes that there is a geographic variation in the species group from East to West. He advances three explanations for this fact:

"(1) The western limestones may be of slightly later date than those in the east.

(2) The assumption of the *disjuncta* habit may have arisen, not so much from an inherent cause, as from some change in the physical environment (for instance, a shifting ocean current) advancing slowly from west to east.

(3) The forms defined as *Zaphrentis disjuncta* may in reality belong to two branches, that prevalent in the

west diverging from the original constricta stock more rapidly than the eastern form."

The density of these corals in a single horizon is on the order of five per aquare meter and presumably the gametes were released into the ocean for distribution as in recent corals, so it would seem probable thatan neighborhood would contain more than 200 individuals. According to S. Wright (1949) this would imply that random differentiation would not be a significantly large factor and Caruthers third hypothesis would be excluded. From the information available at present it is not possible to choose between Carruthers' first and second hypotheses, but the second would seem to be much more probable, since few if any variations such as he postulates in the first hypothesis exist over such a short distance as 90 miles.

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Simpson G.G. (1937) "Patterns of Phyletic Evolution" Geol. Soc. Am. Bull Vol 48 pp 303-314.

Wright S. (1949) "Adaptation and Selection" in "Genetics, Paleontology and Evolution" edited by Jepson G. L., Mayr E. and Simpson G. G. pp 365 to 389.

Table I

Horizon	Carruthers' locality number	#Z.delanouei	#Z.parallela	#Z.constricta	#Z.disjuncta	%Z.delanouei	%Z.parallela	%Z.constricta	%Z.disjuncta	
Millstone Grit	40	-	-	1	19	-	-	5	95	
Calmy (E) Limestone	30	-	-	2	11	-	-	8	92	
	31	-	-	4	14	-	-	22	78	
	33	-	-	19	136	-	-	12	88	
	34	-	-	3	11	-	-	21	79	
	35	-	-	1	6	-	-	14	86	
(C)	37	-	-	5	27	-	-	16	84	Upper Limestone Group of the Carboniferous Limestone Series
	Av.					-	-	15	85	
Extra (E) Limestone	32	-	-	3	7	-	-	30	70	
	36	-	-	4	19	-	-	18	82	
(W)	38	-	1	10	29	-	3	25	72	
	Av.					-	1	24	75	
Hosie Limestone	17	-	4	54	18	-	5	71	24	
	18	-	-	15	5	-	-	[illegible]	25	
	19	1	2	12	3	5	11	67	17	
	Av.					2	5	71	22	
Hurlet (E) Limestone	10	-	-	17	5	-	-	77	23	
	9	-	-	35	9	-	-	80	20	
	8	2	5	106	25	2	3	77	18	
	13	-	-	5	2	-	-	72	28	
	21	-	-	4	2	[illegible]	-	67	33	
	23	-	-	4	5	-	-	45	55	Lower Limestone Group of the Carboniferous Limestone Series
	20	-	-	8	1	-	-	[illegible]	11	
	24	-	-	12	10	-	-	55	45	
	22	-	1	17	16	-	3	50	47	
	28	-	-	3	3	-	-	50	50	
	27	-	-	5	7	-	-	42	58	
	29	-	-	4	7	-	-	36	64	
(W)	26	-	-	32	36	-	-	47	53	
	Av.					-	.5	60.5	39	
Horizon Unknown	11	-	1	18	4	-	4	78	17	
	12	-	1	10	1	-	8	83	8	
	14	2	6	73	12	2	6	79	13	
	15	-	-	16	3	-	-	84	16	
	16	-	2	18	3	-	9	78	13	
Larriston Limestone	2	44	19	-	-	60	40	-	-	
	3	16	8	1	-	64	32	4	-	Cementstone Group
	Av.					62	36	2	-	
Thorlieshope Limestone	4	15	6	-	-	61	39	-	-	

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